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THE BASICRANIAL ANATOMY OF THE NIMRAVIDAE (MAMMALIA: CARNIVORA): CHARACTER ANALYSES AND PHYLOGENETIC INFERENCES

City University of New York PH.D. 1983

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THE BASICRANIAL ANATOMY OF THE NIMRAVIDAE (MAMMALIA: CARNIVORA): CHARACTER ANALYSES AND PHYLOGENETIC INFERENCES

by

NANCY A. NEFF

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1983

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This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

15 August 1983
date

Chairman of Examining Committee
Dr. Richard H. Tedford,
American Museum of Natural History

29 August 1983
date

Executive Officer
James A. Organ

Dr. Leslie F. Marcus, Queens College

Dr. Malcolm C. McKenna, Columbia Univ.

Dr. James Mellett, New York University

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Abstract

THE BASICRANIAL ANATOMY OF THE NIMRAVIDAE
(MAMMALIA: CARNIVORA):
CHARACTER ANALYSES AND PHYLOGENETIC INFERENCES

by

Nancy A. Neff

Advisor: Dr. Richard H. Tedford
American Museum of Natural History

The phylogenetic relationships of the Nimravidae (Oligocene through latest Miocene catlike carnivorans) are controversial: they have been placed either within the family Felidae, or as sister group to the Felidae, to the modern aeluroid Carnivora, or to the Caniformia. Adoption of cladistic analysis is not sufficient to resolve this controversy: all of the last three hypotheses of relationship have resulted from cladistic analyses.

Competing hypotheses of phylogenetic relationship are here demonstrated to be primarily the result of disagreement about the identification and distribution of characters. Such disagreements reflect the need for a rigorous method of character analysis to enable explicit testing of character identifications and distributions--i.e. homologies--prior to a cladistic

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analysis. (In cladistic analysis, characters can be tested only weakly, by inclusion in a cladogram; refutation produces only ad hoc hypotheses, difficult to test). I present a method of character analysis that enables stronger tests of hypotheses of homology by using topological and developmental relationships, prior to simple cladistic analysis, and by using a parsimony criterion to choose among competing hypotheses of character identifications and distributions. Results are compared with examples of persistent errors arising from the uncritical, blind use of homological morphotypes (producing unquestioned identifications, never subsequently tested) and ancestral morphotypes (producing untested polarities). Several problems and inadequacies of cladistic analysis as presently formulated are described, most important of which is the method's inability to distinguish between a true or correct multichotomy and an "unresolved multichotomy".

Detailed analysis of the basicranial anatomy of the Nimravidae demonstrates the value of the method of character analysis formulated here. These odd carnivorans are shown to have lacked any medial branch of the internal carotid artery or a fully ossified bulla, and to have possessed instead a lateral branch of the internal carotid (a "promontory artery"), a peculiar, thick, partially ossified entotympanic, and a separate posterior

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petrobasilar foramen. Many aelurcid synapomorphies exclude the Nimravidae from that group, no synapomorphies place them as sister group to the aeluroids, evidence for any caniform relationship is sparse and contradictory, while overall parsimony places the Nimravidae as sister group to the rest of the Carnivora.

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This work is dedicated

to the memory of

Dr. Everett Lowell Neff.

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INTRODUCTION

A tremendous diversity of catlike carnivorans is demonstrated by fossils primarily from North America and Europe, ranging in age from 38 million years to the Recent (Figure 1). Two major questions may be asked about the taxa constituting this diversity: first, is this assemblage one monophyletic group? And if not, what are the relationships of the separate monophyletic groups within this assemblage with other carnivoran taxa?

Taxonomic History

The first view of this diversity, prior to 1880, and one held by some systematists up to the present day, was that all these forms were closely related to each other and were all properly assigned to the family Felidae (e.g., Pomel, 1853; Leidy, 1869, 1871). Hypotheses of relationships implied by the taxonomic assignments within this family varied widely. However, phylogenetic relationships were not explicitly stated, because it was not yet usual for specific questions of phylogenetic relationship to be directly posed in systematics.

E. D. Cope's (1880a) paper "On the Extinct Cats of America" erected a classification surprisingly similar to some modern ideas for the group but hypothesized a phylogeny quite different from the one implied by his

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classification (when interpreted in modern terms). Figure 2 summarizes both classification and phylogeny. Cope's assignment of Proailurus and Pseudaelurus to his new family Nimravidae was tentative because he had no basicranial material for either genus and could not therefore determine their condition for the exclusively basicranial diagnostic characters that he used to define the families. The phylogeny, based on his statements in the text, correctly relates these two genera to the modern Felidae (see Cope 1880a: 839), but derives the two sabertoothed felids from the nimravid sabertcoths. Thus his classification is essentially a gradistic one relative to his phylogeny, although nearly a phylogenetic one relative to the phylogeny put forth in the present study. This close correspondence of Cope's classification with modern ideas makes his family Nimravidae a convenient designation for use today.

Cope (1880a) initially proposed that the Oxyaenidae (Creodonta) were ancestral to the Nimravidae and Felidae, suggesting specifically (Cope, 1880b:5) that Oxyaena gave rise to the Felidae, whereas the Canidae were thought to have descended from the Miacidae. Later, however, he recognized that the apparent resemblance between the carnassial teeth of oxyaenids and felids was probably misleading, because they were not homologous teeth (Cope 1884: 482). He concluded that the Miacidae (still placed

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by him in the order Creodonta) were the closest to the order Carnivora, based on the homology of the carnassials.

Scott's (1889) discussion of the phylogenetic relationships of the Nimravidae was the next important analysis. W. B. Scott voiced agreement with Schlosser (1888) in considering Flower's (1869) arrangement of the Carnivora on the basis of the basicranial features not to be useful for the fossil taxa; these two workers found that the basicranial features were distributed in a confusing way among the fossils. Part of the confusion doubtless arose from an initial failure to distinguish between useful features (derived character states) and conditions that were merely the primitive state of a more widely distributed character. Much more of the confusion can now be attributed to mistakes in an earlier stage of the character analysis, in the identification of the anatomical features and in basic hypothese of homology. And finally some degree of prejudice seems to have been present, in that the Nimravidae were considered primitive cats from the first, and characters in conflict with that assignment were shown thereby to be misleading:

> "These primitive cats seem to show conclusively that the construction of the base of the cranium has not the taxonomic value attributed to it by Flower (1869) an opinion which Schlosser (1888: 233) has reached on quite different grounds.

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> The basis cranii of Dinictis is perhaps on the whole more cynoid than anything else, though ailuroid and even arctoid features occur."(Scott, 1889: 216)

Scott did make a clear attempt to distinguish between primitive conditions and synapomorphies in his post-Darwinian analysis, and did include some basicranial characters in his discussion. However, he obviously emphasized dental and cranial features, and concluded with essentially a phenetic analysis: Nimravidae have many primitive features, and share some features with Viverridae and some with Felidae, therefore the latter two families must be related to each other if nimravids are closely related to felids, "which no one has ever called in question" (Scott 1889: 240). Figure 3 reproduces his phylogeny, which derives the Carnivora monophyletically from the Miacidae without comment in the text.

Wortman (1892) stated that the Nimravidae were ancestral to the Felidae, but put forth no details of the relationships between individual genera within the two families. He also argued on the basis of dental features that the ancestry of this lineage might be found in the paleonictid creodonts, such as Paleonictis and later Patriofelis.

G. I. Adams (1896) presented a phylogeny with more detail but nearly the same relationships as were in Cope's

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(1880a) phylogeny. Adams' differed mainly in considering Dinictis and Nimravus within the sabertooth group to be each separately derived lines rather than directly ancestral to Hoplophoneus and descendants. However, he no longer recognized a taxon Nimravidae, instead following in part Zittel's (1893) classification: two lineages, the Felinae (culminating in the extant cats) and the Machaerodontinae (comprising the Oligocene taxa and all the sabertoothed forms) were derived, perhaps independently, from unspecified creodonts. Adams based this phylogeny primarily on the characters of the dentition (p. 436), and argued that the basicranial features show parallelism between Smilodon and Felis (p. 443).

The abandonment of the family Nimravidae, begun by Zittel (1893) and Adams (1896), was continued in the North American literature until only recently, largely because of the strong influence of W. D. Matthew's (1910) phylogeny of the Felidae. This phylogeny and corresponding classification are summarized in Figure 4. Matthew derived the modern felids from the non-sabertoothed Oligocene taxa, Dinictis and Nimravus, placing these genera in the Felinae and thus furthering Adams' separation of them from the sabertooth lineage, the Machaerodontinae. The putative common ancestor of the two families was an undiscovered miacid.

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Matthew's extensive discussion emphasized dental features. He quite rightly recognized that Cope had based his family Nimravidae exclusively on primitive features of the basicranium. However, Matthew considered basicranial anatomy only briefly and not in detail, stating that Smilodon was profoundly different from Felis and derived instead "from the primitive 'Nimravid' type, paralleling the true Felines in a few features, wholly distinct or divergent in other." (Matthew, 1910: 298). These features were not described.

One of the few to differ with Matthew was W. B. Scott, whose 1889 discussion has already been mentioned above. He proposed another classification in Scott and Jepsen (1941) but this time did not describe his phylogeny at all clearly. He now recognized three subfamilies within the family Felidae: the Felinae included all the Recent felids and were represented by fossils only as old as the Pliocene in North America and the middle and late Miocene in Europe. His Machairodontinae comprised the sabertoothed 'cats', including Dinictis, Hoplophoneus ("Drepanodon"), Eusmilus, and Smilodon. Cope's "false sabertooths" were recognized as the Nimravinae--Nimravus and questionably Pseudaelurus and Proailurus--and were characterized as being intermediate between the other two subfamilies.

It was Matthew's phylogeny, partly interpreted

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gradistically, that became the basis for Simpson's (1945) widely used classification. The modern Felidae were retained by Simpson in the subfamily Felinae, while the rest of Matthew's Felinae were placed in an expanded Nimravinae and the Machaerodontinae remained intact. Simpson's publication did not include a discussion of diagnostic characters for these groups.

Matthew's phylogeny and Simpson's classification have been the status quo for the cats in North American paleontology until very recently, with perhaps only a single exception. This was Jean Hough's (1953) analysis of the auditory region of the catlike carnivorans and classification of the Carnivora (Table 1). Although in one case a rank was changed, Simpson's Machaerodontinae, Nimravinae, and Felinae remained intact in Hough's classification. The two radical changes proposed by Hough were the separation of the machaerodonts from the felids, and the alignment of the felids (including the Nimravinae) with the canids instead of with the other aeluroids.

In spite of the emphasis on the basicranium in Hough's analysis and discussion. five of the seven categories of diagnostic characters listed for the machaerodonts are dental features. The sixth includes only acknowledged primitive features of the skull, and the seventh comprises the lateral compression of the auditory region and the lack of a true septum bullae. Her

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superfamily Cynofeloidea was diagnosed largely either by admittedly primitive character states or by incorrect homologies: the canoid auditory morphology that she found in the primitive felids (the Nimravinae) consists of character states that are primitive for the Carnivora, or, a more serious problem, misinterpretations of the nimravine anatomy. Furthermore, this canoid morphology of the auditory region is not found in the felines, which are supposedly derived from the nimravines. Matthew's phylogeny for each of the two lineages was apparently still accepted in its entirety.

French systematists throughout this century, in contrast to those in North America, continued to accept both the validity of the association made by Cope of the sabertoothed felids (sensu stricto, e.g. Smilodon) with the other true felids, and the distinctiveness of the nimravids. Piveteau, in his 1931 monograph on the cats from the Phosphorites of Quercy, recognized Cope's family, the Nimravidae, reiterating the basicranial features cited by Cope to define the Nimravidae and Felidae. He also elaborated on Cope's idea of a parallel pattern in the two families, noting within each family a form with small canines (Nimravus and Felis) and a lineage developing large canines (Figure 5). The nimravids, although thought to resemble the ancestor of the felids, were considered by Piveteau not to be directly ancestral to the felids, but

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to have shared a common ancestor with them, and together with them to be most closely related to the viverrids. Teilhard de Chardin (1945) followed Piveteau's analysis but applied the informal names "paleofelids" to the largely Oligocene Nimravidae and "neofelids" to the Neogene Felidae, emphasizing that the latter did not evolve from the former but rather replaced them in the Miocene faunas.

Later, French systematists reduced the rank of the Nimravidae to a subfamily but continued to recognize the two lineages of 'cats' (e.g. Ginsburg (1961), Piveteau (1961), Brunet (1967), or Ginsburg (1979)), as did also the German phylogeneticist, Thenius (1967). This reduction in rank to a subfamily, Nimravinae, within the family Felidae, emphasizes the continuing close association of the nimravids with the felids made by European systematists, although the precise phylogenetic relationships being hypothesized for these two groups are never explicitly stated. De Beaumont (1964) recognized further a separate subfamily for the sabertoothed and non-sabertoothed forms in each lineage, but his phylogenies (Figure 6) differ little if at all from those implied by his colleagues.

The last five years have seen in North America a reevaluation of the phylogenetic relationships among the catlike carnivorans. Tedford (1978) resurrected Cope's

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family Nimravidae, as constituted in Figure 1. He recognized that the nimravids were not closely related phylogenetically to true cats but rather were of problematical relationship to the other feliforms (="aeluroids"). Tedford (pers. comm.) considered them sister group to the modern Aeluroidea--the felids, viverrids, herpestids, and hyaenids--as does Baskin (1981) (position 2 in Figure 7). Martin (1980) has also departed from Matthew's phylogeny to a recognition of the Nimravidae as constituted by Tedford (1978), although Martin still considers them to be most closely related to the Felidae (position 1 in Figure 7). His phylogenetic hypothesis is re-examined below (p. 463) in light of the results of my analysis presented here. Finally, Flynn and Galiano (1982) have proposed a close relationship between the Nimravidae and the Caniformia (="cynoids" plus "arctoids") (position 3 in Figure 7), based on several dental and postcranial characters.

Statement of Problem

The present study was undertaken with the purpose of reevaluating the basicranial anatomy of the nimravids in an attempt to choose on that basis among the three hypotheses depicted in Figure 7. A brief review suggested that earlier confusion over what phyletic relationships were indicated by features of the basicranium was caused

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by two factors: one, the failure by some systematists to distinguish between primitive and derived character states, and two, more often, a mistaken interpretation of the anatomy itself. The realization of the latter problem made clear the need for a detailed study of carefully prepared nimravid basicrania, emphasizing the interpretation of the anatomy in light of the many anatomical studies of this region in extant animals, and also emphasizing the determination of the polarity of the transformation series of character states based on widespread outgroup comparison, and on ontogenetic information when available.

The two questions specifically addressed were:

1) Did any distributions of basicranial characters support either the hypothesis of monophyly of the entire assemblage of catlike carnivorans, or the hypothesis of the monophyly of distinct nimravid and felid lineages?
2) What relationships between the lineage(s) of catlike carnivorans and other groups of carnivorans were implied by the distribution of basicranial characters among the Carnivora and their outgroups?

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MATERIALS

Specimens.--Fossil carnivoran skulls with well preserved, fairly complete basicrania are very uncommon; this paucity of specimens has been worsened by hasty or inexpert preparation. Almost all specimens used in this study had been incompletely prepared before careful preparation by either Mr. Otto Simonis or myself. Complete preparation permitted the determination of structures previously overlooked or misconstrued; very careful preparation provided confidence that no foramen or groove is an artifact of rough preparation.

Most material is from the collections housed in the Department of Vertebrate Paleontology of the American Museum of Natural History in New York. The institutional abbreviations used in the text are:

AMNH -- American Museum of Natural History, Department of Vertebrate Paleontology

AMDM -- American Museum of Natural History, Department of Mammalogy

ANSP -- Academy of Natural Sciences of Philadelphia

F:AM -- Frick American Mammals collection, housed in the Department of Vertebrate Paleontology, American Museum of Natural History

LACM -- Los Angeles County Museum

USNM -- United State National Museum

YPM -- Yale Peabody Museum

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UF -- Florida State Museum, University of Florida

All available material currently in the AMNH collection was examined. The nimravid and other carnivoran material selected for preparation and detailed study, and separately described below, is listed in Table 2.

Taxonomy.--No effort was made to identify unidentified specimens to species, nor was a taxonomic revision within the Nimravidae undertaken. The goal of this study was to characterize the nimravid basicranium, and to determine what phylogenetic relationships of the family were indicated by that characterization. This requires the assumption that there is a group Nimravidae about which to ask the question. Even this asumption was treated as a hypothesis to be tested: if special features were not found to characterize such a group and derived characters were found instead uniting at least some of the constituent taxa with various other taxa outside such a group, then the initial assumption of monophyly would have been contradicted. My goal would then be to determine the separate relationships of the constituent taxa. An initial assumption of monophyly for each constituent taxon would then be necessary, and would be tested by the analysis in the same fashion.

Initially, however, no assumption of the monophyly of any genus is required, even though the descriptive anatomy

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is presented below by genus. The genera as here constituted form phenctypically rather coherent groups, contributing to the ease of description. Whether each genus is monophyletic or polyphyletic will make no difference either to the descriptions, which are tied to specific numbered specimens, or tc the significance of any given character in the determination of the family's relationships. If a genus is actually polyphyletic, we should find either that that genus has no defining characters but is morphologically entirely primitive relative to another genus or genera, or that one or more species within this polyphyletic genus is seen to share derived character states with the members of another genus or other genera. But neither situation would affect either the analysis of the basic basicranial anatomy of the Nimravidae (or separate, monophyletic subgroups if that turns out to be the case), or the analysis of the family's or separate groups' relationships.

It is true that the lack in most cases of multiple specimens of each species prevents assessment of how much variation seen within a genus is information that might be taxonomically useful at the specific level (interspecific variation) and how much merely reflects intraspecific variation in that feature. But again, this is relevant only to a taxonomic revision within the family and not relevant to an assessment of the phylogenetic

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relationships of the Nimravidae as a whole. If a feature is variably present, whether inter- or intraspecifically variable, it is almost certainly not useful for a determination of the family's relationships; that variation will be determinable from the descriptions as they are presented here.

A variety of Recent specimens, and some other fossils in addition to those studied in detail and listed in the first table, were examined to confirm my understanding of the characters, and to a lesser degree, to check the determination from the literature of each character's distribution within the Carnivora and in out-groups for the order. These specimens are listed in Table 3.

Classification:--The following classification of the Order Carnivora is intended to provide definitions (i.e., included groups) of the higher taxa used in the following discussion, and to give some idea of the relationships among the taxa mentioned, especially those used for comparison. It is more detailed than the working hypothesis of phylogeny shown in Figure 7. The classification is also more conservative than the phylogeny however: I have generally (but not always) avoided adopting names for higher groups when they included only isolated families, for example, and have implied multichotomies when I consider the evidence for specific relationships to be even more tenuous than is

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generally the case.

The standard classification for nearly forty years has been Simpson's (1945). However, his classification reflected both gradistic and cladistic concepts--an approach that is not intrinsically incorrect per se. However, such a mixed approach has not been found to be entirely satisfactory to many of us who are particularly interested either in phylogenetic relationships or in maximally informative classifications (in the sense not of how much information "went in" to a given classification, but how much can be retrieved accurately from a given classification) or in both. Given the latter criteria, I prefer a classification that reflects the better supported phylogenetic hypotheses, but includes multichotomies for remaining problems, and whose overall hierarchical structure is entirely consistent with the phylogeny. Thus, the classification given here (rather than Simpson's (1945) classification) is used in the belief that it will enable me to summarize character distributions better and refer more simply to natural groups.

Most of the classification of the groups in the Caniformia follows Tedford (1976) for the higher levels, and an unpublished cladogram by Tedford, distributed in 1980. However, within the Caniformia, I place the Amphicyonidae close to the Ursidae, in contrast to Tedford's placement of them as sister group to the rest of

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the non-miacid Caniformia (equivalent to position 3 on the cladogram in Figure 7). My reason for this is primarily the large excavation into the basioccipital for a large inferior petrosal venous sinus in both Amphicyonidae and Ursidae. This issue is discussed further by Hunt (1974b, 1977). The division of the "miacids" sensu lato is after Flynn and Galiano (1982), although, as will be obvious later, this arrangement raises some questions about the evolution of ear morphology within the modern Carnivora.

The relationships and subgroups within the Feloidea (the four extant families) are based on my own preliminary analysis. The resurrection of the division of the 'viverrids' sensu lato into the two families Viverridae and Herpestidae has been confirmed and greatly amplified by Chris Wozencraft (in prep.). A number of special features are shared by Hyaenidae and Felidae on the one hand, and by Hyaenidae and Herpestidae on the other; I do not think either set sufficiently overwhelming in light of the other to resolve the trichotomy indicated. Some of the subfamilies indicated also represent problems: the Stenoplesictinae, now in the Viverridae, may be either paraphyletic or sister group to the entire Feloidae. Cryptoprocta may actually be related to the Herpestidae and Hyaenidae. within the Felidae, I recognize an Acinonycinae but within it I include Uncia (snow leopard) as well as the cheetah, and a couple of fossil taxa cn the

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basis of several aspects of skull morphology. Pantherinae comprises only P. leo, P. pardus, P. tigris, and P. onca, primarily on the basis of the specialized hyoid for roaring, a condition I hypothesize does not occur in Uncia. The other "big cat", Neofelis, is placed in Felinae incertae sedis, as is Puma.

order Carnivora Bowditch, 1821

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plesion fam. Nimravidae Cope, 1880

subfam. Nimravinae Cope, 1880

subfam. Hoplophoninae Kretzoi, 1929

subfam. Barbourofelinae Schultz, Schultz, and Martin, 1970

suborder Feliformia Kretzoi, 1945

infraord. Aeluroidea Flower, 1869

plesion fam. Viverravidae Wortman and Matthew, 1899

superfam. Feloidea Hay, 1930

fam. Viverridae Gray 1821

subfam. Stenoplesictinae Schlosser, 1923

Viverrinae Gray, 1821

Paradoxurinae Gray, 1864

Cryptoproctinae Gray, 1864

fam. Hyaenidae Gray, 1869

subfam. Ictitheriinae Trouessart, 1897

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Hyaeninae Gray, 1869

Protelinae Geoffroy, 1851

fam. Herpestidae Bonaparte, 1845

subfam. Herpestinae Bonaparte, 1845

Hemigalinae Gray, 1864

Galidiinae Gray, 1864

fam. Felidae Fischer, 1817

subfam. Proailurinae Zittel, 1893

Felinae Fischer, 1817

Pantherinae Pocock, 1917

Acinonycinae Pocock, 1917

Machaerodontinae Gill, 1872

suborder Caniformia Kretzoi, 1945

plesion fam. Miacidae Cope, 1880

infraord. Cynoidea Flower, 1869

fam. Canidae Fischer, 1817

subfam. Borophaginae Simpson, 1945

Caninae Fischer, 1817

infraord. Arctoidea Flower, 1869

plesion fam. Amphicyonidae Trouessart, 1885

subfam. Daphoeninae Hough, 1948

Amphicyoninae Trouessart, 1885

parvord. Ursida Tedford, 1976

superfam. Ursoidea Gray, 1825

fam. Ursidae Fischer, 1817

subfam. Amphicynodontinae Simpson,

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1945

Hemicyoninae Frick, 1926

Ursinae Fischer, 1817

Ailuropodinae Grevé, 1894

fam. Otariidae Gray, 1825

subfam. Enaliarctinae Mitchell and Tedford, 1973

Desmatophocinae Hay, 1930

Otariinae Gray, 1825

Odobeninae Allen, 1880

parvord. Mustelida Tedford, 1976

superfam. Procyonoidea Bonaparte, 1850

fam. Procyonidae Gray, 1825

subfam. Simocyoninae Dawkins, 1868

Ailurinae Gray, 1843

Bassariscinae Gray, 1869

Procyoninae Gray, 1825

superfam. Mustelcidea Swainson, 1835

fam. Mustelidae Fischer, 1817

subfam. Mustelinae Fischer, 1817

Melivorinae Gray, 1865

Melinae Bonaparte, 1838

Guloninae Gray, 1825

Mephitinae Bonaparte, 1845

Taxidiinae Pocock, 1920

Leptarctinae Gazin, 1936

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Lutrinae Bonaparte, 1838

fam. Phocidae Gray 1821

subfam. Semantorinae Orlov, 1831

Phocinae Gray, 1821

Monachinae Gray, 1869

order Creodonta Cope, 1875

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fam. Oxyaenidae Cope, 1877

fam. Hyaenodontidae Leidy, 1869

fam. Palaeonictidae Zittel, 1893

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METHODS

Introduction

Since the first question that led to this study was one of phylogenetic relationships, the methodology employed should be one that produces and evaluates evidence for hypotheses about phylogenetic relationships. Much recent discussion in the systematic literature has dwelt on the various methodologies in systematics. That cladistic analysis is the appropriate method for constructing hypotheses of phylogeny from character distributions is widely recognized (Mayr 1974; Simpson, 1975). However, "cladistic analysis" is not monolithic: arguments about details of the theoretical structure of the method, or about which algorithms are the appropriate ones for cladistic analysis, certainly still occur, as do also arguments about the entirely separate question of the appropriateness of cladistic classification (vs. classification on any basis other than sequence of phylogenetic relationships alone).

My purposes in this discussion are threefold: 1) to state briefly which version of cladistic theory and methodology was employed in this study, 2) to present some discussion and criticism of cladistics that, to my knowlege, have not yet been fully put forth elsewhere, and

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3) to describe in detail the methodology I have formulated to repair the primary deficiency of cladistic analysis--a method of character analysis.

Because my goal is the elucidation of phylogenetic relationships, a cladistic analysis was perfcrmed. Such an analysis may be summarized as the construction of a hypothesis of group membership based on the distributions of characters among the included taxa, and the testing of that hypothesis by comparisen with the distributions of additional characters. That this is the appropriate method for deriving phylogenetic relationships has lcng been recognized, at least among paleomammalogists. For example, W. B. Scott asserted in 1889 in a discussion of the phylogenetic relationships of the Nimravidae that "It is obvious, in the first place, that the retention of primitive characters in any two groups of a series is no proof of any relationship nearer than that through the common ancestor of the entire series." (p. 231). Of course, a thorough analysis of primitive versus derived character states was not always performed (as discussed in the Introduction). And it was much rarer for entirely vertical classifications, if any were proposed, to be constructed. In the present study, questions of classification are reserved for brief discussion in the last section; my primary goals are the description of the basicranial anatomy of the Nimravidae, an analysis of the

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phylogenetic relationships of the family, and a discussion of the methods of character analysis which facilitate such a phylogenetic analysis.

General philosophical basis.--The philosophical basis of our scientific methods has been much discussed in the systematic literature in recent years. This discussion is valuable for two reasons: 1) knowing exactly what we accept as valid reasoning enables each of us to monitor our own reasoning and thereby reduce facile acceptance of interpretations on insufficient evidence; 2) stating our procedures clearly in communicating our results provides others a firm basis from which to accept or doubt our interpretations. Some very skilled systematists may be able to study their organisms and frame phylogenetic or other sorts of hypotheses in an entirely logical fashion without ever having to evaluate their methods of reasoning. I suspect these people are rare exceptions and that most if not all would benefit as I have from careful thought about their methods.

The philosophical literature, at first glance, presents a contrast between the theoretical philosophers of science, who devise and evaluate schemes for how science should be done, and the sociologists of scientific philosophy, who present generalizations about how science is done. There seem to be some differences in the conclusions of the two camps. Thus the researcher is left

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with the question: how does one know which is the right way to do science? The review and discussion that I have found most useful is that by Lakatos (1970), in which the methodology proposed is evaluated by its correspondence to the apparent methodology of successful science in the past. (The question then regresses to one of evaluating the 'success' of various past research programmes, or even of science in general. I will merely accept Lakatos' evaluation for the purposes of this study.)

Brief introductory discussions of the philosophical allegiances of many cladists can be found in Gaffney (1979) or Wiley (1981). Most of these discussions espouse a method that Lakatos (1970) labels "naive methodological falsificationism". In this approach, acceptable hypotheses are those that are testable or "falsifiable"; progress is made by diligently searching for refutation of such hypotheses. I have found this characterization of how science is properly done inadequate, and prefer instead to evaluate phylogenetic methodology in the context of a philosophy dubbed "sophisticated methodological falsificationism" by Lakatos. Discussion of the philosophical context of my methods will be limited to those aspects particularly important for understanding later specific points about cladistic analysis; a more thorough analysis of both types of methodological falsificationism can be found in Lakatos (1970) and

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numerous references cited therein.

Our knowlege about anything is uncertain. There is no absolute proof of anything, including the low-level (very specific) hypotheses we typically call "facts" and usually treat as certain. One of the points that will be substantiated by my study is that the current practice of systematics has been to treat hypotheses of too high a level of generality as facts, which are then not readily subject to question and possible refutation. Demonstrable error has arisen from this practice.

Our assertions about a subject can be stated in several ways. First, a distinction must be made between hypotheses and assumptions (part of what Lakatos (1970) terms "unproblematic background knowledge"). Within a given study, if an assertion is treated as an assumption, that assertion is not subject to testing and possible refutation by the evidence (i.e. by lower-level, or more specific, hypotheses); the assumptions are taken as true during the interpretation of that evidence. An enormous number of "facts" are assumed to be true in any study. Most are not called into question far enough even to be labelled assumptions and be thereby acknowledged as potentially open to doubt. In other words, stated assumptions are usually restricted to those items of "unproblematic background knowledge" that are not 'obviously' true and might therefore be most profitably

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considered problematic in another study.

In contrast to the assumptions, the statements framed as hypotheses are those that are subject to test within the structure of the study. By this is meant that from the hypotheses can be deduced specific expectations that can then be observed to be "true" or "false". It must be remembered, however, that these observations are themselves hypotheses (usually lower-level hypotheses) and never known absolutely to be true or false. As a result no hypothesis can be absolutely disproven any more than it can be absolutely proven. (For this reason, I use the terms "to refute" and "refutation" rather than "to falsify" and "falsification"; the former implies a decisive marshalling of evidence against an assertion but need not be taken as absolute disproof, whereas the connotation of "to falsify" is more absolute. I will restrict "refutation" to the step of abandoning a hypothesis (when it is replaced by a better one, even temporarily), and will use the term "contradiction" to describe the inconsistency between an 'empirical observation' (i.e. a lower-level hypothesis) and the currently held hypothesis under test. This distinction between contradictions and refutations is an important one in sophisticated methodological falsificationism. It is discussed briefly below, and in more detail by Lakatos (1970).)

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In naive falsificationism, a hypothesis is tested by congruence or incongruence between the deductions from that hypothesis and the "facts"--hypotheses that are of a lower level of generality and therefore almost always more highly corroborated. Hypotheses of the same level of generality can be incongruent with each other, but this would seem to be a weaker test of any given hypothesis because all could be roughly equally well corroborated and one falls back on considering corroborated the largest subset of hypotheses congruent among themselves from the entire group of hypotheses--a sort of consensus. This is a form of the parsimony criterion and is actually in widespread use.

The concept of parsimony is a much discussed and often misused one. This discussion will be limited to a single caveat: parsimony is a criterion applicable to our constructs about the world, not to reality itself (for example, Crisci's (1982) "methodological" versus "ontological" parsimony). Reality is neither parsimonious nor nonparsimonious; evaluations of whether reality could be simpler than it is are impossible since we neither <u>know</u> fully what reality is nor can we judge whether something that is not real but apparently simpler <u>could</u> in fact exist. Instead, it is our explanations of reality, our hypotheses, which are either parsimonious or nonparsimonious, which entail either a greater or lesser

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number of assumptions and auxiliary hypotheses. Thus my use of "parsimony" corresponds to Crisci's "methodological parsimony"; I consider his concept of "ontological parsimony" nonsensical.

A maximally parsimonious hypothesis is the simplest one available that best fits the most data. The problems with using this concept are most easily seen by observing that the preceding statement includes three entities or qualities (the definitions of all of which are open to argument) to be maximized simultaneously: "simplest", "best fit", and "most data". Inclusion of the last item, "most data", incorporates the original concept that hypotheses or explanations are not to be multiplied unnecessarily. An extension of this concept leads to the criterion of (tentatively) accepting the 'least refuted' hypothesis (or the maximally congruent subset) from a set of competitors, because, were that hypothesis (or set of hypotheses) accepted, the fewest number of ad hoc hypotheses (to explain the anomalies) will be required. In many cases, the relative parsimony of hypotheses will be a complicated matter to judge, often depending on how one counts up the anomalies requiring auxiliary hypotheses and perhaps on assumptions about the likelihoods of various events (weighting anomalies as stronger or weaker contradictions). (For example, see the discussion of weighting characters and of the relative likelihoods of

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alternative transformation series in the section below on character analysis.)

In any event, a hypothesis is corroborated or contradicted by the available evidence, but neither corroboration or contradiction is absolute. As a result, the possibility remains that a refuted hypothesis may regain preferred status if the refuting evidence (i.e. anomalies that gained the status of counter examples) is itself independently refuted (that is, 'empirical observations' are found to be 'wrong' and the replacement hypothesis therefore comes to be contradicted by the data), or if there are a limited number of hypotheses that can conceivably be held about a circumstance and all others are more extensively contradicted. In the latter case, the evidence incongruent with the least contradicted hypothesis is itself (tentatively) discarded (refuted by the higher-level hypothesis); that is, these contradictory 'empirical observations' become the anomalies that are explained by auxiliary or ad hoc hypotheses.

Both Lakatos (1970) and Kuhn (1970) have pointed out that hypotheses usually coexist in our body of knowledge with observations that contradict them. The observations are either not interpreted correctly (i.e. not recognized as contradictions--the influence of the assumptions held at any time) or, more usually, are explained by an auxiliary hypothesis and then disregarded because the main

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hypothesis is otherwise well corroborated. In the latter case, the initial (incongruent) interpretation of the observation is therefore considered wrong (reflecting the failure to come up with a better main hypothesis to fit more of the observations including this contradiction). However, such a lower-level hypothesis should not be considered refuted by the accepted higher-level hypothesis it contradicts. It remains an anomaly until it is refuted directly by revising the interpretive theories used to produce the 'empirical observation' (and there are always such theories and assumptions) or by gathering additional still lower-level 'empirical observations' to justify a re-interpretation under the same interpretive theories.

In very simplified summary, productive and useful studies are structured (implicitly or explicitly) such that they divide a large hierarchy of hypotheses about the world into three levels:

1. assumptions -- higher-level hypotheses taken to be true during the study
2. hypotheses -- the hypotheses being tested in the study
3. data, facts, or empirical observations -- lower-level hypotheses taken to be true in order to test the hypotheses in the study

The focus can and should be moved up or down, so that what is assumed in one part of a study is tested in another, so that hypotheses serve sometimes as "facts" to test

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higher-level or more general hypotheses and other times as hypotheses themselves to be tested by even lower-level hypotheses. At any level, a hypothesis must predict certain empirical consequences, which can be 'observed' to be 'true' or 'false'--that is, about which lower-level hypotheses can be made.

Naive methodological falsificationism holds that a hypothesis can be refuted by contradictions between the predicted empirical consequences of the hypothesis and the actual observations. However, since contradictions to almost all hypotheses are known, often from the moment of adoption of a hypothesis, it would not appear productive to simply discard all otherwise useful hypotheses without better alternatives. And it is difficult to establish an arbitrary decision procedure to determine when contradictory observations are sufficient for refutation. Sophisticated methodological falsificationism provides the answer: contradictory empirical observations alone, even when well corroborated, are never sufficient to refute a hypothesis. Instead, a hypothesis is considered refuted when it can be replaced by a better one--when it can be replaced by a hypothesis that explains more about the world, one that explains everything the old hypothesis explained plus some of the empirical observations that were anomalous under the old hypothesis. This difference in refutation--by accumulated 'empirical observation' or

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by more successful hypothesis--is the primary difference between naive and sophisticated falsificationism.

These philosophies and their ramifications are discussed in much more detail by Lakatos (1970) and references cited therein. Let us merely summarize here the points that will be most important in the following discussions of cladistic analysis and character analysis:

"Contrary to naive falsificationism, no experiment, experimental report, observation statement or well-corroborated low-level falsifying hypothesis alone can lead to falsification. There is no falsification before the emergence of a better theory." (Lakatos, 1970: 119, emphasis omitted). "...falsification is not simply a relation between a theory and the empirical basis, but a multiple relation between competing theories, the original 'empirical basis', and the empirical growth resulting from the competition." (Lakatos, 1970: 120).

Adherence to sophisticated falsificationism is reflected in the usage of "refutation" and "contradiction" stated earlier: empirical observations may contradict a hypothesis, but we consider that hypothesis refuted only by the acceptance of a scientifically better one. The criteria for the better hypothesis are: 1) that it must predict or explain previously unexplained facts (excess empirical content), 2) that it explains all the unrefuted content of the previous hypothesis, and 3) that some of

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the excess empirical content of the new hypothesis be corroborated. (Lakatos 1970: 116).

An auxiliary hypothesis, a clause added to a hypothesis to accommodate anomalies, may be scientific and progressive (if it predicts consequences in addition to the anomaly it was designed to explain), or an auxiliary hypothesis may be a non-scientific ad hoc hypothesis (without excess empirical content). The first, the progressive auxiliary hypotheses, add to the information content of the hypothesis, whereas the second, the ad hoc hypotheses, merely decrease the parsimony of the main hypothesis without contributing to its scientific (testable) content.

Phylogenetic Analysis.--The term "phylogenetic analysis" is used here in a broad sense, comprising character analysis, cladistic analysis, and macroevolutionary analyses, thus covering several hierarchical levels of hypotheses. For example, a well corroborated phylogeny may be used as a "fact" in the generation or testing of some higher-level hypothesis, such as the biogeographical affinities of a region or a macroevolutionary hypothesis. And, although character analysis proper has been generally overlooked, there has been a general recognition that the character distributions used to test phylogenies are themselves lower-level hypotheses and can be true (homology) or false

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(homoplasy or convergence). For the problem at hand, that of the phylogenetic relationships implied by nimravid basicranial anatomy, both character analysis and cladistic analysis will be employed.

Character analysis is the construction and testing of character distributions--hypotheses of homology--individually, prior to any hypothesis of phylogeny. Thus, put in the context of the three levels in scientific studies summarized above, the main hypotheses being tested are those of character identifications and homologies, and the empirical observations (lower-level hypotheses), upon which these main hypotheses are based, are the observed topological relationships among structures, the form and detailed construction of structures, the ontogeny of structures, and the functional (mechanical) actions of structures. Character analysis is discussed in much more detail below.

Previous discussions of "phylogenetic analysis" usually considered cladistic analysis primarily if not exclusively. In cladistic analysis, hypotheses of the sequence of phylogenetic relationships among some taxa (relative recency of common ancestry) are constructed and tested. A hypothesis of phylogenetic relationship is constructed from an initial set of character distributions and is tested by the concordance of additional character distributions with the phylogeny. The basic structure of

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the hypotheses in cladistic analysis is a three-taxon problem: given three taxa, which two are more closely related to each other than either is to the third? (Following Cartmill (1981) with slight modifications, phylogenetic hypotheses will be summarized using parentheses: the hypothesis "((AB)C)" is that taxa A and B are more closely related to each other than either is to taxon C.) Cladistic analysis provides a test of character distributions in that characters that contradict an unrefuted hypothesis of phylogeny are themselves considered refuted: they are anomalies and are explained by ad hoc hypotheses of convergence or reversal.

In this discussion, I am using the term "character" in a strict sense: a character is a complete set of homologous features. This is equivalent then to "shared derived character" or "synapomorphy". "Primitive character" is a misnomer, because what is meant by it is only a particular state or expression of a character, part of a character and not an entire character. For example, if vertebrate taxa A and B have scales, and taxon C has feathers, it is illogical tc talk of a character "scales" in A and B versus the character "feathers" in C if the two features are considered homologous at some level--that is, if feathers are considered modified scales. It is true that the presence of scales does not evidence ((AB)C), but not because "the presence of scales is a primitive

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character" but rather because the character "scales" characterizes (ABC), i.e. has a higher level of distribution than just a group (AB): "feathers" is a special case of the more general character "scales".

Determining such character distributions is a problem of character analysis; the 'fact' that feathers are modified scales is a hypothesis to be tested in character analysis. For this reason, it is useful to speak of character states, in this case the states "scales" and "feathers". Character states do not always have ontological reality, but do have a heuristic value and a practical use in the analysis of hypotheses about characters. In our example, the character hypothesis would be that "feathers" and "scales" are states of the same character, and that that character is "scales", i.e. that "scales" as a character comprises the primitive state "scales" (i.e. unmodified scales) and the derived state of "scales" called "feathers". This usage, while not particularly necessary to cladistic analysis as typically performed to date, is fundamental to my study because character analysis, which has a predominant role here, requires such a rigorous explicitness of language.

Some confusion has arisen in the past from a careless use of the concept of character state. Two extremely important points must be kept firmly in mind. First, during character analysis one may not know which character

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states are real (i.e. equal to characters) and which are fragments of a character, because both conditions could be encountered. That is, hypotheses of homology may not be formed yet, or the character state tree (= transformation series) may not be worked out yet. Thus the distinction between characters and character states is important: the tentative status of character states must be kept in mind. Second, the absence of a feature is commonly said to be a character state (in contrast to the feature's presence), particularly in coding for a numerical analysis, but in fact "absence" is a universal character state, being possessed by every organism in at least the early stages of ontogeny, and therefore, by a generality or out-group criterion, always the primitive state. "Absence" can never be a character, although of course "loss" can be.

Cladistic Analysis

The specific mechanics of cladistic analysis as typically performed have been summarized in Gaffney (1979), Eldredge and Cracraft (1980) and Wiley (1981), and will not be repeated here. For an extended exploration of the various nuances of branching diagrams, see Nelson and Platnick (1981). Most of these references also cover well the extension of cladistic analysis to higher level hypotheses such as evolutionary hypotheses or biogeography. However, I consider them variously

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incomplete in their description of character analysis--the derivation and interpretation of data used to construct and test cladistic hypotheses; this portion of phylogenetic analysis is discussed in detail below. The present study also differs from these presentations of cladistic analysis in that these previous discussions did not incorporate the precise usage described above of "character state" and "character", and all described a philosophy that may be identified with that termed naive methodological falsificationism by Lakatos (1970).

Assumptions.--Any study in which a hypothesis is constructed and evaluated requires that some body of relevant knowledge be treated as "unproblematic background knowledge" (Lakatos 1970: 106ff.). Therefore assertions that cladistic analysis requires no assumptions, or only two assumptions, and so forth, are clearly in error. It may be true that, if the hierarchy of groups produced by cladistic analysis is not interpreted as a phylogeny, then the assumption that evolution occurred and produced the hierarchy of groups that we are discovering is indeed not made. But even in a non-evolutionary context, unless the philosophy of the cladist advocates some sort of inductive methodology, there must be an assumption that a hierarchy exists in nature and that the character distributions used in cladistic analysis have some sort of necessary relationship to the hierarchy.

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Gaffney (1979) lists two assumptions made when the hierarchy is interpreted as phylogeny; these are modified here as:

1) The taxa in the set under study all share a common ancestor, from which these taxa have descended.
2) This genealogy has been accompanied by heritable changes in the morphology of the organisms.

These are not the only assumptions, however: many assumptions exist, but an exhaustive list of assumptions for any study would be difficult if not impossible to compile. Much background knowledge is seldom questioned; examples in this case might be the assumption of the reality and recognizability of the taxa in the study, the assumption that characters are stable enough to generalize from a sample to an entire taxon, and so forth. A third assumption generally made (e.g., Simpson, 1961, although oddly interpreted therein) should be stated distinctly here because later argument will be based upon it:

3) The evolution of life on earth has proceeded in general from simple to complex by the addition and elaboration of features, and from initially low diversity to high cumulative diversity.

One other assumption is coming under increasing question and might therefore also be profitably added to our formal list:

4) Homologies are recognizable as such often enough to

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enable the deciphering of phylogeny from the "noise" of convergence and reversals.

This last assumption is a specific version of a very common assumption--that our observations are what we think they are often enough that our conclusions are right more often than not, i.e. that our mistakes are not so frequent that they negate progress. This sort of assumption is usually so basic that it is not stated. However, in phylogenetic reconstruction it is being increasingly called into question in response to the resistance of some phylogenetic problems to solutions.

Structure of the Analysis.--Given these assumptions, the basic form of the hypothesis under test in cladistic analysis is the three-taxon statement, of the form ((AB)C), and the predictions it makes are that characters will be found with the distributions (AB) and (ABC), and more significantly, no characters will be found with the distributions (AC) or (BC). (It is important to remember the strict use of the term "character" in this analysis, described above.) Contradictory observations, characters apparently distributed (AC) or (BC), are considered anomalies, and explained by the ad hoc hypothesis of convergence (i.e. interpreted as two characters with distributions (A) and (C), or (B) and (C)) or reversal (i.e. interpreted as two characters, the first distributed (ABC) and the second, the loss of the first feature,

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distributed (B) or (C)). Contradictory observations are treated in this fashion until a sufficient number of them result in the hypothesis (A(BC)) or ((AC)B) having more content (and requiring fewer *ad hoc* hypotheses) and therefore becoming the preferred hypothesis.

Criticisms of cladistic analysis have not, to my knowledge, been directed against the methodology as outlined here, but instead have been based either on an implicit disagreement with the underlying scientific methodology or on a misunderstanding of the basic structure of cladistic analysis. For example, although Cartmill (1981) states that he has accepted for the purposes of discussion the methodological falsificationism espoused by most cladists, his initial argument contradicts the tenets of even naive falsificationism. He makes the assertions (p. 76), for example, that single uncorroborated observations (single contradictory character distributions) falsify hypotheses of relationship. Furthermore, his discussion implies an absolute falsification, coming closest to what Lakatos (1970) terms "dogmatic falsificationism".

Cartmill's subsequent arguments have some additional problems that also appear to be rooted in a very different view of scientific methodology. Discussion here may help emphasize the significance of a clear philosophical context for our phylogenetic methodology. For example, in

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cladistic analysis an assumption of the nonsensical concept of "ontological parsimony" (Crisci's (1982) term) in evolutionary history is not required to study phylogenetic relationships ("the claim that evolution has always operated in the most economical way possible to produce the observed phenetic differences among organisms." (Cartmill 1981: 78, original emphasis).) Even for Cartmill's restatement of the hypothesis under study (p. 78), all that is needed is some form of the third assumption listed above--that no matter where the path of evolutionary history has wandered, we will be able to follow it by recognizing homologies correctly more often than not.

Cartmill's question "How many characters of our taxa must we examine before we can claim that a given 3-taxon hypothesis has been falsified?" is a very good one, and emphasizes one of the problems with the statement of falsificationism made in the cladistic literature to date: naive methodological falsificationism does require some sort of decision procedure to demarcate anomalous observations from refuting observations. The difficulty and arbitrariness of this procedure is one of the strongest arguments for sophisticated methodological falsificationism (which is what is actually employed in most cladistic analyses, even if the cladists do not say so explicitly). Under this philosophy, Cartmill's

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question would be answered thus: "No number of observations can refute a hypothesis. A hypothesis can only be refuted by a better hypothesis." (See p. 32 above.)

Cladistic analysis is usually said to include the procedure of "out-group comparison"--the determination of primitive versus derived character states (the "polarity" of the "character", or better, of the set of homologous character states) by comparison with taxa outside the monophyletic group of taxa under analysis. The character state that occurs outside the group under study is the more general one and therefore hypothesized to be primitive relative to any state(s) occurring only within the group. Simpson considered this procedure to be a strong source of evidence for polarity but seemed unaware that a priori knowledge of the phylogeny is clearly implied: "Perhaps the most conclusive evidence as to primitive (and hence ancestral) characters is provided when one condition in a group or one end of a sequence has a homologue in another group of more remote common ancestry." (Simpson, 1961: 102, emphasis added.) Out-group comparison is considered part of the basic structure of cladistic analysis: for example, Wiley (1981: 110) states that the basic system is three-taxon trees and the out-group. Determination of polarity by out-group comparison for each character is usually what is

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meant by "character analysis" in cladistic discussions.

In contrast to the usual treatment of out-group comparison, I will distinguish two kinds of out-group comparison, both of which are steps in different forms of cladistic analysis. These two kinds are respectively: 1) determination of the relative generality of distribution of character states by examining a set of taxa larger than the monophyletic group within which phylogenetic relationships are being determined, and 2) the rooting of a network of relationships among a set of taxa by the designation of one taxon as the out-group. Although the first kind of out-group comparison is often called "character analysis", I include it within cladistic analysis because it requires, as does the second form of out-group comparison, a priori knowledge of a phylogeny, to decide which taxa are out-groups and which are within the group under study. I restrict the term "character analysis" to individual analyses of sets of homologous character states without any assumption of known phylogenetic relationships.

To understand the close relationship between these two forms of out-group comparison and the position of each procedure in cladistic analyses, we must first be very clear about how the various components of a cladistic hypothesis are related to the data from which the hypothesis is derived. The two components of a cladistic

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hypothesis are the topology of the network among the taxa, and the position of the root in that network that produces the tree. ("Network" and "tree" are used here, as in most of the systematic literature, in a sense opposite to their meanings in graph theory.) That these are two separate components can be seen by studying Figures 8 and 9.

Four different networks can be formed for four taxa (Figure 8). From each of these four networks, numerous trees can be formed, each corresponding to a different placement of the root of the tree (Figure 9). This is significant because a collection of character states, for which hypotheses of homology have been constructed (producing the inclusive sets of homologous character states usually called characters) but for which hypotheses of polarity have not been constructed (which would produce the nested sets of informative characters), will be best fitted by one network. (We will ignore the complication of ties due to noise in the data set, and the lack of an algorithm to produce the known shortest tree other than by exhaustive search--the Steiner tree problem.) An example is shown in Figure 10. This hypothetical data set is most parsimoniously explained by the network shown. Thus the choice of this network over any of the others is based entirely on phenetic similarity; the polarity of the characters (i.e. recognition of characters versus non-informative character states) is irrelevant to this

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choice. (This network is called a Wagner network in the numerical cladistic literature, e.g. Kluge and Farris, 1969.)

A network for a set of taxa can be rooted in two ways, corresponding to the two aspects of out-group comparison mentioned earlier. If one taxon is designated the out-group, the resultant tree would be that one with the out-group placed as the sister group of all the rest (example I in Figure 11). This is equivalent to hypothesizing that the character states in that taxon are all primitive relative to those in the taxa under study.

Alternatively, the network may be rooted by a character-by-character analysis, determining the characters within each set of homologous character states by examining the distribution of the character states in a variety of additional taxa to determine which states are the most generally distributed and therefore primitive. The combination of these primitive character states forms a "mock ancestor", an artificial taxon to serve as the out-group. (This artificial taxon is called the "morphotype" by several authors, but that term has other meanings and is avoided here because of its ambiguity.) The result could be indistinguishable from example I in Figure 11 if one taxon happened to have all primitive character states, or the real taxon in the out-group position could now have some derived features relative to

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the rest of the taxa (example II). A final possibility with a character-by-character analysis of polarity is that conflicts may arise, even though the network perfectly fits the data set. Example III in Figure 11 illustrates this possibility. Such conflicts are resolved either by ad hoc hypotheses of convergence or reversal in the character(s) (a refutation of some of the lower-level hypotheses of homology within the sets of homologous character states) or by reversing the presumed polarity of the incongruent character(s) (a refutation of the lower-level hypothesis of polarity).

Both methods of rooting the tree involve designating out-group taxa, and therefore require an assumption of known phylogeny to the extent that the monophyly of the group under study is thought known, so that out-groups can be recognized as such. Often a more detailed phylogeny is assumed: chosen out-groups may be specifically those thought to be the sister groups of the group under study. This assumption is commonly made in cladistic analysis.

The assumption of a higher-level phylogeny is not required if one recognizes that methodological parsimony requires that we interprete the evolutionary history of life as having gone in general from the simple (organisms with fewer characters) to the complex (organisms with more characters). This is required by methodological parsimony because the opposite hypothesis, complex to simple,

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requires additional explanations for the origin of the complex organisms in the first place. It must be emphasized that this assumption does not forbid neoteny or the loss of features (a derived character state); the assumption is only that, on the whole, evolution has been from simple to complex more often than not. It can then be seen that the polarity of some features can be recognized without any form of specific out-group comparison: a feature for which no homologues can be found in any other taxon is a character defining the group comprising those taxa in which the feature (including all modifications thereof) is found.

Novelty and restricted distribution constitute one of the criteria for determining polarity in character analysis, discussed further in that context beginning on p. 78. Re-examination of our earlier example will illustrate the significance of this criterion for our understanding of cladistic analysis. Upon reconsidering the data set in figure 10, let us say we find that the open square and circles symbolized the absence of any feature homologous to that symbolized by the closed squares and circles. Absence of a feature can not be a character; the data set is better depicted as in Figure 13. Characters 1 and 2 define groups (ABC) and (AB) respectively, implying the cladogram shown. Of course, incongruities in the distributions of such characters

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would require the *ad hoc* hypothesis of reversal or convergence; in this case reversal would be the *loss* of a feature, a derived condition in contrast to the primitive condition, *absence*. And hypotheses of relationship constructed without out-group comparison are as testable as any other: a sufficient number of additional characters may be contradictory such that an alternate hypothesis becomes preferred.

Recognition of groups on the basis of novel characters permits the hypothesizing of phylogenies within the context of which one may analyze the polarity of states in additional characters. This higher-level hypothesis is assumed for out-group comparison within its included taxa, but can itself be tested by additional relevant characters. Cartmill's (1981: 85ff) arguments against the assertion that phylogenetic hypotheses can be assessed at different levels are fallacious for two main reasons. First, he overlooks two important aspects of scientific methodology: that tests are provided by *additional* empirical observations and that assumptions made in one analysis can only be tested by a separate analysis. In the case of phylogenetic analysis, any hypothesis of relationship can be refuted if a sufficient number of additional characters are found to contradict the hypothesis under test and are better explained by another hypothesis. However, *within* a given analysis, any

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hypothesis assumed to be true for that analysis will not be locally testable (it is an assumption) and will indeed affect the outcome of the analysis (it would not be a relevant assumption if it did not). Secondly, the occurrence of local optima--hypotheses of relationship that are parsimonious for a restricted set of taxa but are no longer parsimonious when the character distributions over a wider set of taxa are considered--is a good example of one situation calling for the replacement of a hypothesis by a better one, one that explains a larger number of character distributions for more taxa with fewer total ad hoc hypotheses. Although such steps may be unacceptable in dogmatic or even naive falsificationism, it is exactly how progress is made under sophisticated falsificationism.

In summary: out-group comparison is not required for cladistic analysis when novel characters (or characters determined by other criteria in character analysis) are known for the groups. Out-group comparison may still be useful as a short cut to determine the polarity within more complex characters (sets of homologous character states); this is discussed further in the section below on character analysis. In either case, the topology of the network best summarizing the character distributions over taxa is independent of the identification of characters with each set of homologous character states,

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i.e. independent of the polarity of the characters. This permits segregation of the contribution to the cladogram of the distribution of character states (hypotheses of homology) from the contribution of the hypotheses of polarity.

Ancestors.--A surprising amount of emphasis has been placed on arguments about identifying ancestral taxa. If taxon A has no novel characters relative to taxon B, i.e. if the character states in A are entirely primitive relative to those in B, then yes, A might be ancestral to B. This is, strictly speaking, testable, since a character unique to A would make more acceptable the hypothesis that A is merely the sister group of B. However, ancestry is a weak hypothesis in that a single erroneous 'empirical observation' will result in falsely accepting or rejecting it. Since I see no uses for hypotheses of ancestry that cannot be served equally well by hypotheses of phylogenetic relationship, and the possibility of undetectable error is high, I have not constructed hypotheses of ancestry for any of the taxa in my study.

Character weighting.--Numerous procedures have been proposed to enable the information in some sets of character states to contribute more to the resulting phylogenetic hypothesis than do others (e.g., Hecht and Edwards, 1976; Kluge and Farris, 1969; Sneath and Sokal,

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1973, and references cited therein). Character weighting is intended to increase the likelihood of deducing the true phylogenetic relationships. Its efficacy is therefore dependent on the degree to which we can estimate the likelihood of a character state tree to be free from errors in homology and ordering. None of the arguments put forth to date convince me of any method's ability to do this.

Part of the difficulty with arguments about the likelihood of convergence in a given feature is that it appears dangerously easy to argue both ways in many cases, and thus difficult to apply the principles objectively. For example: "Intricate adaptive complexes are unlikely to arise twice in exactly the same way, hence to be convergent in two occurrences, and the probability of homology is greater the more complicated the adaptation and the closer the identity." (Simpson, 1961: 89) versus "convergence is to be suspected when groups resemble each other only or most closely in some way specifically adaptive to a particular, shared ecology and are otherwise different." (Simpson, 1961: 91).

As has been pointed out before, some de facto weighting results merely from the act of using a feature in the analysis or not, from the number of states into which we divide it, or even from the number of sets of character states into which a complex of features is

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divided. The truth of this observation only serves to emphasize the importance of character analysis, the need to describe explicitly the evidence for identifications or character state trees, and the great importance of a procedure to test the character hypotheses independently of their use in a cladistic analysis. Character weighting is only an issue to the degree that we are making mistakes in character analysis: it is an attempt to estimate in the analysis of which features mistakes are more likely and in which less likely, and to place more emphasis on the latter. Surely it is better to reduce error by more intensive and sophisticated character analysis than to accomodate error.

Problems with Cladistic Analysis.--Cladistic analysis as currently employed does have some methodological problems, even when considered in the context of sophisticated methodological falsificationism. One such problem lies in the view of phylogenetic hypotheses as progressive or degenerating in terms of Lakatos' problemshifts. Rather than being a linearly progressive series of hypotheses of relationships, there is only possible a rotation among a finite number of possible hypotheses: ((AB)C), ((AC)B), or (A(BC)). The only progress can be said to occur in the expansion of the data base--the number and variety of 'empirical observations', in this case characters, that are relevant to the

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hypotheses. Cladistic analysis by itself does not appear to be a very powerful scientific research programme (Lakatos, 1970). The problem is probably that cladistic analysis is only a set of methods, or at most just one level in a systematic hierarchy. However, the multiple levels in phylogenetic analysis as here characterized do provide room for continued development of our understanding of the interaction among the processes made relevant via our interpretive theories to each level, and among the resulting phenomena at different levels.

Secondly, the inability to seriously propose multichotomies as testable hypotheses raises doubts about how closely we are approximating the true phylogeny and may limit the usefulness of phylogenetic hypotheses in macroevolutionary questions. A single observation (a character distributed (AB), (BC), or (AC)) is enough to make the hypothesis (ABC) less informative than ((AB)C), (A(BC)), or ((AC)B) respectively. But this means that a single mistake in our hypotheses of character distributions either way can make the difference between (ABC) and one of the specific, dichotomous hypotheses. (This is logically equivalent to the problem with hypothesizing ancestors: an ancestor might be expected to have no unique characters. However, one mistake--either overlooking a character unique to the putative ancestor or incorrectly restricting a character's distribution to the

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putative ancestor--will result in either incorrectly accepting or incorrectly rejecting the hypothesis of ancestry.)

Our confidence that we will make progress in spite of some mistakes about specific homologies arises from the accommodation in the system to some contradictory observations. Now, if one is willing to assume that phylogeny has been entirely dichotomous with character change in each branch at speciation, that ancestral taxa became extinct when they gave rise to daughter taxa, and that we do not sample these ancestors (e.g. Figure 13 A), then the inability to treat multichotomies as hypotheses is no problem: the correct cladograms will be dichotomous (Figure 13 B). But that requires fairly restrictive assumptions about the nature of the evolutionary process and raises doubts about whether cladistic analysis as currently formulated could give information appropriate to testing alternative hypotheses about patterns of speciation.

The phylogeny in Figure 14 C is a realistic example under some theories of speciation and morphological transformation: one example might be a model of strong genetic homeostasis in large populations, and rapid evolution restricted to small, speciating peripheral isolates. Were all the characters interpreted correctly, then the resulting hypothesis of phylogeny would include

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large multichotomies as shown (Figure 14 B). Furthermore, if some mistaken hypothesis of homology were used as an 'empirical observation', such as mistakenly considering character ÷ in H to be the same as character + in I and J, then the cladogram would be (incorrectly) further resolved, as in Figure 14 C. Thus the danger is in not being able to distinguish between correct multichotomies and unresolved multichotomies, especially if one is interested in using the phylogenetic hypotheses resulting from cladistic analysis in choosing among alternative patterns of speciation or in answering other macroevolutionary questions. More careful character analysis is not a satisfactory answer to this problem because the basic structure of the hypothesis in character analysis is a "three-taxon" problem as well: the only way to refute the character hypothesis that ÷ and + are the same character would be by demonstrating that ÷ shares instead more significant attributes with a character in G that logically precludes its homology with +, which is logically equivalent to refuting (G(H(IJ))) by demonstrating ((GH)(IJ)). (GH(IJ)) can never be as informative as either, and will never be the surviving hypothesis in a competition. The inability of cladistic analysis to distinguish between correct multichotomies and unresolved multichotomies is currently an unsolved problem.

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After this discussion was written I enccuntered Fortey and Jeffries' (1982) paper in which are presented additional examples of phylogenies with unresolvable multichotomies, unresolvable if one is restricted to using only the distribution of shared derived features. Although the thrust of their argument is in a different direction from that of my points above, they do suggest (without supplying details) that the solution to a slightly different problem, that of determining the true sequence in spite of the lack of character evolution in the ancestral lineage, is to be found in stratigraphic and paleontological information.

Three additional points are directed more at the practice of cladistic analysis than at its theoretical structure. The first is a caveat: ad hoc hypotheses of convergence or reversal are often followed by a re-examination of the features in the taxa involved and a subsequent discovery of apparently corroborating differences between features originally thought more specifically homologous. There are two dangers here. First is the failure to realize that the ad hoc hypotheses are not actually testable, in that similarities are not really admitted as contradicting the hypothesis of reversal or convergence; one merely speaks of a more complete convergence. Only negative evidence could be said to contradict such an ad hoc hypothesis--the failure

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to find any differences--and that is, of course, not a useful way to construct a hypothesis. Therefore it is safer to consider ad hoc hypotheses of convergence or reversal not to be directly testable.

The other danger in accepting apparent corroboration of reversals or convergences is that such contradictory characters may then be considered resolved and no longer kept in mind as potential counter-evidence to the currently held hypothesis. For progress to be made, anomalies under the current hypothesis must be kept in the forefront of the analysis. Thus it is important in this context to keep a record of hypotheses about each character state tree. A character may be contradicted by a cladogram, and its character state tree revised, but the evidence for the original interpretation of the character is still evidence against the accepted cladogram and should not be discarded. If a given cladogram has required the revision of several character hypotheses, one may suddenly find that the cladogram should be considered refuted rather than those character hypotheses revised, if an alternative hypothesis of relationship becomes a better one.

On a practical level, a cladogram would be tested by the addition of new characters to the original data matrix (not to the suite of character hypotheses including the revisions made to conform to the currently accepted

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cladogram), the best-fit cladogram found for the expanded set, and then that new cladogram compared with the one being tested. This is rather difficult to do in practice, especially for published hypotheses of relationship, unless the character analysis step is kept separate from the cladistic analysis so that the a priori character hypotheses are always available. Regrettably, the usual procedure of "reciprocal illumination" has been to replace some of the original character hypotheses with revised hypotheses made in response to contradictions with the best-fit cladogram. The symptoms of this can often be seen in the published reports of cladistic analyses: until quite recently, the a priori character hypotheses were not even discussed. Rather the characters to support each node were described as if no polarities were ever revised; frequently convergences or reversals were not mentioned. Recently there has been an increasing move to report modifications in hypotheses of polarity made in response to the cladistic analysis, or the existence of convergences and reversals (often accompanied by expressions of surprise at the high amount of convergence); these are laudable but will always be difficult and awkward as long as character analysis is not explicitly recognized as a separate procedure.

A second practical point for cladistic analysis is the suggestion that the pattern of contradictory character

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distributions be clearly summarized. The degree to which a hypothesis of phylogeny is rendered dubious by a certain number of contradictory characters might be considered to be dependent on whether most contradictions suggest a single alternative hypothesis or whether there is little consensus among the contradictions. A closely related idea is the basis for Farris' (1969: 374) method of character weighting: "characters that are reliable for cladistic inference are those that are consistent with the true phyletic relationships...Cladistically unreliable characters can be hierarchically correlated only by chance."

The third practical problem is the actual construction of the cladogram that best explains the character distributions, i.e. the shortest tree for that data set. This step is usually much more easily stated than done: character conflicts often suggest many alternative trees for a given set of characters. If the characters and taxa are at all numerous, determination of a short tree for the data can be very difficult, and without assurance that it is the shortest tree, or one of a set of equally shortest trees. The problem of identifying minimal-length trees is currently being studied (e.g., Foulds et al., 1979). Of course, the ideal solution is to have very few character conflicts in the data set; in such cases, the best-fit cladogram is easily

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derived. To obtain such a solution requires that characters be re-analyzed and tested thoroughly prior to the derivation of the cladogram--a practical argument in favor of the testing procedure in character analysis presented below.

Finally, we come to perhaps the most significant deficiency in cladistic analysis as currently formulated and practised. As Schaeffer et al. (1972: 36) noted a decade ago, "In practice, most paleontologists (like most neontologists) assume specific homologies, and question their validity only if no phylogenetic sense can be made of the data." However, both naive and sophisticated versions of falsificationism suggest that the 'empirical observations', especially ones taken as counter-evidence, should themselves be corroborated. Cladistic analysis still offers only the higher-level hypothesis of phylogeny as a 'test' of character distributions and does not really enable true corroboration. What is needed is a lower-level scheme of testing, independent of the hypotheses of phylogeny, a method that focusses on the hypotheses of homology and polarity as the main hypotheses, to be tested in turn by 'empirical observations', relatively lower-level hypotheses. This testing procedure is provided by an expanded method of character analysis.

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Character Analysis

The solution to several of the problems with cladistic analysis lies in development of a method of character analysis that will focus on the construction and testing of independent hypotheses of character distribution. Not only does the theoretical discussion of cladistic analysis outlined above demonstrate the need for a rigorous method of character analysis, but also there is evidence for this need in the persistent controversy over specific questions of relationship. Disagreements about relationships occur even when there is apparently agreement about phylogenetic methodology, implying that the source of the disagreement is not resolved by cladistic analysis. (Of course, some arguments about classification appear superficially to be arguments about relationships, but are not what are being discussed here if, as is often the case, the disputants would draw identical phylogenies for the taxa about whose classification they are arguing.) So why do disagreements over phylogenetic relationships persist? Because phylogeneticists frequently do not agree on the character distributions being used to construct the phylogenies: they do not agree on the identifications, weighting, and polarities of the characters in the data set being used to construct or to test hypothesized phylogenies.

That the source of controversy over phylogenies must

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be disagreement over character distributions is obvious when one remembers that the topology of the network minimally accounting for the different character states is determined solely by the distribution and ordering of those character states. Three criteria provide information about the relative distributions (polarity) of the characters independent of any phylogenetic hypothesis, with the result that the network can be at least partially and usually completely rooted to form a tree or cladogram on the basis of the results of character analysis alone, obviating or reducing the need for out-group comparison and its assumption of a higher-level phylogeny. And, of course, at the most general level, rooting can only be on on the basis of such independent criteria because one eventually runs out of out-groups. Thus the configuration of the best cladogram is largely or entirely determined by character hypotheses constructed prior to cladistic analysis even if all out-group comparison is considered part of cladistic analysis. Differences in the interpretation of the morphology will result in differences in the phylogenetic hypotheses. Agreement merely on the method of cladistic analysis is not sufficient to eliminate discordance among the phylogenetic hypotheses constructed for a group.

This great importance of character analysis has been generally overlooked (with a few notable exceptions, e.g.,

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Bock, 1977). Current discussions of systematic methods frequently treat characters as given, using in their examples merely letters, numbers, or symbols (as was done above), or obvious homologies that are not readily questioned by the reader (e.g., bird wing and tetrapod forelimb); they describe only briefly if at all how hypotheses of homology are arrived at, and none proposes appropriate tests of homology, tests other than the consensus of numerous characters--the phylogeny, a higher-level hypothesis. (An extreme example is found in Nelson and Platnick (1981); the closest approaches to what I consider a complete and useful discussion are in Bock (1977) and Wiley (1981), but the latter still lack a fully testable scheme prior to the cladistic analysis.)

Even when systematists, especially paleontologists, concentrated on morphological change as the main theme of evolution, the emphasis was on reading the morphological trends (in an adaptational context) from a phylogeny, rather than being critically aware of how the phylogeny was being derived from morphology (in some cases in conjunction with stratigraphy) in the first place. A recent awareness of the importance of the cladogenetic aspect of phylogeny (e.g., Eldredge and Cracraft, 1980) has shifted emphasis away from this former sort of transformational view of characters, appropriately enough for the taxic view of evolution useful for working with

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higher-level hypotheses, such as macroevolutionary questions. But this emphasis needs to be balanced and indeed supported by a new awareness of the crucial importance of morphology in developing specific hypotheses of phylogeny, which must inevitably engender an increasingly conscientious and meticulous methodology of character analysis.

An appropriate and useful methodology of character analysis would be one in which the hypotheses of homology were treated as the central hypotheses in the analysis (level 2)--that is, an analysis in which homologies among specific features 1) were hypothesized based on some 'empirical observations' (lower-level hypotheses), 2) were tested by additional 'empirical observations', and 3) were considered refuted only if a better hypothesis of the homologies for those specific features were found. To what extent is this sort of analysis provided by the current procedure? The first step is generally followed, as will be recognized from the description below. An explicit testing of homologies by additional pertinent lower-level hypotheses is not often done, and an explicit weighing of conflicting evidence for alternate hypotheses of homology even more rarely, if ever, performed. Alternative hypotheses are proposed, to be sure; they are the source of the disagreement discussed above. But the conflict between interpretation of morphology is rarely

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addressed at the level of morphology rather than phylogeny, although when it is, a clarification of the issues and the anatomy often occurs. Instead, most alternative hypotheses for characters are the ad hoc hypotheses of convergence or reversal erected in response to conflicts within a particular phylogeny. As implied by the designation of them as ad hoc, they do not serve as better hypotheses for those features as called for in the third criterion listed above, but instead are constructed only to save that higher-level hypothesis of phylogeny.

The method of character analysis presented here is an attempt to meet the three criteria given above and extend scientific methods in systematics to questions of homology and morphology. As was the case with cladistic analysis in systematics, the method itself is not new, but in my estimation is what the best anatomically oriented systematists have always done. However, as was also the case with cladistic analysis for phylogenetic reconstruction, a formal and explicit description of this method of character analysis will increase the ease with which new systematists learn to do character analysis, the degree to which experienced systematists adhere to useful and logical methods in their research, and the effectiveness with which all systematists communicate the results of their anatomical and phylogenetic studies.

Introduction to the method of character

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analysis.--Figure 15 outlines the major steps in character analysis and cladistic analysis. Each of the four levels (labelled I through IV) represent levels at which hypotheses can be constructed, which are then testable by the evidence of the preceeding step, and which in turn test the hypotheses at the following level. An awareness of this hierarchy is necessary for the recognition of when evidence does or does not constitute a valid test of a given hypothesis, a recognition that has been lacking in many descriptions of phylogenetic analysis.

Although the two steps in character analysis have not been performed as temporally distinct steps in the past, nor need they be in all cases, separating them and discussing them as distinct steps will aid our analysis of the assumptions or interpretive theories used to interprete the 'empirical observations' that serve as evidence in each step of character analysis. For the present discussion, I have refrained from dissecting step 1 into still further separate steps, although it could be done, because I did not find that any informative subdivision of the interpretive theories or kinds of evidence resulted from such a deccmposition. Step 1 therefore comprises both the discerptive procedure of recognizing separate, distinct character states and the agglomerative procedure of recognizing homologues, clustering character states into sets comprising different

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conditions of the same features. Thus step 1 may be considered essentially a definition and identification step.

Step 2 is the determination of the polarity of the character states, recognizing primitive versus derived states, and ordering them into character state trees. If only the general descriptions are considered, the distinction between the two steps appears rather arbitrary: step 1 can be described as the recognition of character states and the grouping of those character states into the largest unnested sets possible, whereas step 2 is the subdivision of these most inclusive sets of homologues into nested subsets (equivalent to the character state tree), in which each set constitutes a character. However, one of the most important points demonstrated in the following discussion is the distinct difference in the evidence, interpretive theories, and ad hoc hypotheses for each of these two steps. Table 4 summarizes, for each of the steps in character analysis, the activity and product of that step and the nature of the ad hoc hypotheses used to explain anomalous results in the light of the currently most parsimonious cladistic hypothesis.

A note may be made here of a problem that will be discussed more fully in the analysis of the basicranial features in my study: the uncritical use in the past of a

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morphotype or archetype as a restrictive interpretive theory in character state identification and character state tree construction. Assumptions about "the primitive condition for mammals" have often strongly influenced the interpretation of mammalian anatomy, especially of fossils. Rather inflexible concepts of what structures must be present in a species identified as an early member of a given group, concepts approaching an idealistic archetype or bauplan, have hampered character analysis, and, as a result, biased the results of cladistic analysis. Emphasis in this study is placed cn a detailed and explicit discussion of how character analysis can be done to bring to the surface (and thus expose to evaluation) some of these restrictive assumptions previously employed.

Before beginning the detailed discussion of character analysis, it will be useful to reiterate the difference between characters and character states, and to state the goal of character analysis in these terms. Characters are hypotheses of homology: a character is a set of all the features, however modified, that we hypothesize to be derived from one feature in the common ancestor of all taxa exhibiting the character. This is the <u>definition</u> of character or homology; criteria for the recognition or identification of specific characters are very different from the definition of the concept (Ghiselin, 1966; Bock,

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1977). Indeed, criteria for recognition of characters must be independent of and without reference to any concrete phylogeny if the characters so identified are to be useful (i.e., non-circular) evidence for the phylogeny of the taxa under study. But the interpretive theories for evaluating evidence for homology, for recognizing homologies in practice, must be based on assumptions about phylogeny and evolution in general if the recognition of homologies is to be relevant to deriving cladistic hypotheses.

Characters are nested sets of features. This is the logical basis for Bock's (1973, 1977) point about homologies requiring a conditional clause (e.g., bird wings and bat wings are not homologous as wings but are homologous as tetrapod forelimbs). A character state is a specific, describable condition (the hypothesis from step 1 in character analysis), which may be a complete character or may be only one condition of a character. Thus in Figure 16, a2 is a character state with the same distribution as the character A2, while a3 is the primitive character state within the character A3 (which comprises both states a3 and a4). Characters are determined from the character state tree. For example, four characters can be delineated on the tree in Figure 16, in the hierarchy depicted by the nested set diagram in Figure 16C.

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Character state trees are constructed by hypothesizing polarities for pairs of character states (step 2 in character analysis): which state is primitive and which derived. Again using the example in Figure 16, this character state tree would be the result of evidence that a1 was primitive relative to all other states, that a3 was primitive to a4, and that a2 was derived relative to a1 but not part of the derived sequence containing a3 and a4. Sources of such evidence are discussed in detail in the section below on step 2 of character analysis.

The present discussion is sufficient to support several conclusions. First, determining the relative polarities within a set of character states is equivalent to constructing a character state tree (step 2 in character analysis). Secondly, the complete distributions of characters are only recognizable in the context of a character state tree, so that derived character states are not omitted from the delineation of a character; such an omission would leave an incomplete character, frequently labeled in the current literature with the misnomer "primitive character".

The hierarchical relationships among characters results in characters having distributions of different generalities: some characters are more general and include less general, or more specific, characters. (All these characters imply corresponding more or less

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inclusive monophyletic groups, of course.) In this context, it can be seen that a 'primitive character' is actually part of a more general, more widely distributed character. It is important to recognize that the term "general" when applied to a character in this analysis refers only to its relative generality of distribution across taxa. "General" in this sense does not imply "undifferentiated ontogenetically," or that the taxon is a generalist ecologically, for example.

An interesting parallel with cladistic analysis may be noted here. As Hecht and Edwards (1977) have pointed out, there is the possibility that none of the observed states is primitive, that the sampled character states all arose independently from an unrepresented primitive state. This is equivalent to the true multichotomy in cladistic analysis and is similarly impossible to distinguish from the merely unresolved multichotomy. Paleontology may be the best source of help here because the fossil record is certainly likely to contribute more homologous character states, and those states (not taxa) are more likely to be relatively primitive. (This point was made indirectly by Simpson (1961: 84-86) and recently emphasized by Patterson (1977b: 625): "the contribution of paleontology is not ancestral organisms but ancestral character states.")

One question treated as a problem and discussed in the literature is how characters or character states are

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delimited. Hecht and Edwards (1976) argued that nine features that had been analyzed as nine separate sets of homologues were actually all one character: paedomorphosis. But as illustrated by their argument, that revised character hypothesis is a more parsimonious one that can be safely adopted only after the nine features were analyzed separately and seen to have the same distribution. Therefore, in this study, anything recognizable and describable is a feature; the most parsimonious character hypotheses are the result of a continual search for more parsimonious, more explanatory character hypotheses.

In the context of this rigorous understanding of character states, character state trees, and characters, the goal of character analysis can be simply stated: it is to determine the identity and distribution of characters. Given the above definition of a character, it is evident that characters (and not character states) are our sole source of evidence for phylogenetic relationships. This distribution of a character across a set of taxa is evidence that that set of taxa shared a common ancestor not shared with taxa lacking the character. (It may be briefly noted that "loss" is a derived character state within a character, usually recognizable only under an ad hoc hypothesis equivalent to reversal, and therefore not the same character state as

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the universally primitive character state "absence".) Each character is evidence for a hypothesis of monophyly, which can be tested by comparison with other such hypotheses of monophyly in cladistic analysis. But note that in cladistic analysis the hypothesis of monophyly is what is being tested, in that it can be refuted--replaced by a better supported hypothesis of monophyly; the definition or distribution of the character implying that hypothesis is not directly tested, in that alternative hypotheses of monophyly are not sufficient to refute the character hypothesis by replacing it with a more parsimonious character hypothesis. (The widespread failure to recognize this distinction has been responsible for much of the present failure to resolve character conflicts adequately.) If the hypothesis of monophyly indicated by a character is refuted by other characters, the ad hoc hypothesis is that something must be wrong with that character, which really calls into question the content and application of the interpretive theories used to obtain that character. But only additional character analysis could enable one to refute the original character hypothesis, since the ad hoc hypotheses generated under cladistic analysis are not themselves usefully testable (see pp. 100ff). The rest of the discussion of character analysis further supports the reasoning behind these assertions, and provides a method for profitably testing

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character hypotheses.

Step 1: Determining character states.--Most of the sources of evidence for delineating characters, differentiating character states and deciding which belong together in a set have been thoroughly reviewed in numerous discussions of characters and homology (e.g., Jardine, 1969; Kluge, 1971; Mayr, 1969; Simpson, 1961; Sneath and Sokal, 1973; Wiley, 1981; Zangerl, 1948), and actually are little extended in basic principle beyond Owen's (1847:174) brief criteria for homology. Some of the main kinds of evidence have been briefly listed in Figure 15. They are all criteria for deciding whether structures are comparable or not: whether two features in different organisms are made of the same kind of tissues, whether the parts or details of structure correspond, whether they are in roughly the same topological relationship to other comparable features, whether their similarity in composition, details of structure, and topological relationships extend back throughout the ontogenetic history of the feature, or through time and space in its biomechanical action ("function" fide Bock and von Wahlert, 1965).

All comparable features that correspond so closely in detail that they cannot usefully be distinguished, except at the level of individual variation, may be said to constitute one character state. A complete set of

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character states comprises all known variations of comparable features, forming (for the taxa under study) the largest possible set of homologues. Numerous and usually rather specific interpretive theories are used at this stage to decide what are usefully considered comparable features and what are so different that they are no longer comparable, especially theories about what sort of evolutionary changes are possible based on current notions of epigenetic mechanisms. Examples of such theories may be found in the character analysis of the nimravid auditory region described below (pp. 365, 379, etc.).

Refutations of the hypotheses formed by this step occur more frequently than one might immediately realize: every decision that some feature has been misidentified and every re-identification is a refutation of one such hypothesis by another. This step and the hypothetical nature of identifications are perhaps more obvious for fossils than for extant material, because of the variable preservation of fossils and because the sources of evidence are usually restricted to details of structure and topological relationships with other skeletal elements.

Step 2: Ascertaining characters.--Characters may be defined as monophyletic groups of character states. In order to use characters to find the phylogeny of a set of

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taxa, however, one must have criteria for recognizing monophyletic groups of character states, criteria that can be applied independently of any assumed phylogeny for those taxa, preferably independent even of the most spare phylogenetic assumption, that the taxa under study form a monophyletic group relative to one or more out-groups. (Some authors, for example de Jong (1980), have failed to realize that merely a statement of monophyly is a statement about phylogeny. It is not a very detailed phylogeny, but it is nevertheless a statement of higher-level phylogeny since monophyly is defined in terms of phylogeny. Recognition of this point is important in evaluating criteria for determining polarity; failure to recognize this point has resulted in errors in previous analyses.) There are at least three sources of evidence for polarity that do not require an a priori phylogeny. These are listed in Figure 15.

The simplest, and in some ways most important, criterion is that of relative novelty. If a subset of the taxa under study has some feature, and one can find no homologues of it in the remaining taxa, the most parsimonious interpretation is that absence is the primitive condition and that the feature is a character uniting those taxa in which it is observed. This is a logical conclusion from the third assumption on p. 40; it follows from the assumption that the present diversity is

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the result of a phylogeny. Of course, mistakes in identifying the states are possible: one might mistake "loss" for "absence". In some such cases, ontogenetic information may differentiate these two conditions by demonstrating a transitory development of a feature absent in the adult (e.g., teeth in baleen whales (Arnold, 1981) or at some loci in Tarsius (Luckett and Maier, 1982)), whereas in other cases, the re-identification of a condition as "loss" rather than "absence" may be an ad hoc hypothesis, discussed below. But the criterion of novelty is nevertheless valid, if one accepts the basic assumption that the overall trend in the evolution of life has been from nothing to something, from simple to complex, from initially low diversity to high diversity.

Novel features, "presence/absence characters", are the most widespread and generally useful in the determination of phylogenies. For example, a form of relative novelty in details of 'complex characters' has apparently been the implicit criterion by which branching in character state trees has been recognized. Sets of more than two character states are often ordered or linked in an unrooted network on the basis of overall similarity (a procedure discussed critically below, on p. 116). More usefully, some sort of "special similarity" within the 'complex character' states can serve as a logical basis for recognizing subsets within a total set of character

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states. Such subsets can be expressed as a character state tree, within which the character states are ordered and linked. This form of the method is somewhat artificial and needlessly complicated, however, since all such details of 'complex characters' can be sorted out as characters relevant to a specific level of generality, i.e., characterizing a subset of taxa. In terms of trees, this is reflected in the fact that all trees with more than two states, no matter what their topology, can be resolved into a set of several two-state trees, which then include as separate characters the special similarities that previously defined subsets of states. (This is the logical basis for additive binary coding.) Because of this equivalence, the discussion here will be largely in terms of deciding the polarity of pairs of character states, although it is undeniably often heuristic and useful in practice to combine related features into complex characters and summarize them in character state trees comprising more than two states.

The distribution of character states throughout the ontogeny of the taxa under study is another criterion for ordering character states in a tree. Although discussions of ontogeny as a source of evidence often become elaborate (e.g., Nelson, 1978), the basic useful point can be put quite simply: the variation in morphology through ontogeny is another source of information about the

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distribution or relative generality of character states within the taxa in question. If the ontogenetic sequences were observed as in Figure 17A, character state a1 would be seen to be completely general and a2 to have a more restricted and therefore informative distribution. The simplest explanation is that a1 was the condition in the common ancestor of XYZ, and a2 is a specialized condition restricted to the descendants of the common ancestor of YZ.

In Figure 17B a more complicated example is proposed to illustrate that the sequence of states in ontogeny is not relevant: the relevant information is the generality of the distribution of each character state. Thus in this example, state a2 is seen to be more general, and either a1 or a3 or both of restricted distribution, representing one or two embryonic adaptations. If we consider the specific example listed, it becomes clear that the more general distribution of a2, the association between the chorionic and allantoic membranes, is the main basis for the identification of the trophoblast of mammals as homologous in some sense with the chorion of reptiles. The relative generality of a1 versus a3 would have to be determined from other evidence. But the distribution of character states over the ontogenies of the three taxa has demonstrated the more general distribution of a2 in spite of the sequence in which the character states appeared

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within ontogeny.

Neoteny is sometimes held up as a phenomenon that invalidates the use of ontogenetic evidence in determining the polarity of character states, the generality of characters. But as was the case for unique features, discussed above, "loss" can be mistaken for "absence": neoteny can be mistaken for the primitive absence of a specialized feature. Once this equivalence is seen, it becomes clear that neoteny is a derived condition just as any other sort of "loss" is (p. 50). And also as with any loss of a feature, the identification of neoteny is an ad hoc hypothesis erected to save some cladistic hypothesis that is contradicted by the character distributions as originally hypothesized. Neoteny is no more, and no less, of a problem to the use of ontogenetic evidence than is the possibility of reversal a problem to the use of evidence from adult morphology.

(Recognition that neoteny is merely an ad hoc hypothesis of loss makes it clear that it is no more of a "falsifier of ontogeny" than reversal or loss is of comparative anatomy--if one finds useful the idea of "falsifying" a method anyway. Nelson's (1978; Arnold, 1981; Nelson and Platnick, 1981) problem with neoteny evaporates. His analysis suffers from two primary flaws: first, contrary to his usage, "Neoteny" is not a source of evidence in the set comprising "Ontogeny", "Anatomy", and

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"Paleontology". Neoteny is an ad hoc hypothesis, not a method, and logically should not be treated as of the same status. Second, within his analysis of the generality of characters, "loss" is not distinguished from "absence".

Finally, there is an interesting misinterpretation in Nelson's discussion (1978) of the significance of the ability to induce metamorphosis hormonally in the axolotl. Responsiveness to growth hormone is neither incongruent nor corroborative of the hypothesis of neoteny: if the axolotl had not responded it would not have contradicted neoteny because it could have neotenously lost even the ability to respond. Responsiveness to the hormone, while certainly congruent with several possible theories of genetic and hormonal control of metamorphosis, only tested and indeed strongly contradicted a hypothesis that the axolotl was incapable of developing adult features, not a particularly useful hypothesis in this analysis. This is an example illustrating the insusceptibility to test of the ad hoc hypotheses of loss.)

Oddly enough, the use of ontogenetic evidence suggested here--as a source of evidence about the relative generality of character states without regard to sequence--has to my knowledge never been proposed before. All previous ontogenetic criteria have been based on the sequence of character states. The classic recapitulationist argument was that the sequence of forms

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in ontogeny directly paralleled the sequence of forms in phylogeny. Nelson and Platnick (1981) recently revived this concept, trying to argue that the sequence of states in ontogeny gives direct information (i.e. without reference to a higher-level phylogeny) about polarity: "features that appear early in development can be considered primitive relative to the modifications of those features that appear later in development" (ibid., p. 37). However, their justification from parsimony is completely valid for the ontogenetic criterion I have here proposed, without any need to invoke the sequence of states as part of the analysis.

In the same work, Nelson and Platnick (1981: 332) repeated Nelson's (1978: 327) restatement of the biogenetic law: "given an ontogenetic character transformation, from a character observed to be more general to a character observed to be less general, the more general character is primitive and the less general advanced." Careful consideration reveals that this statement is true but trivial. It was shown above that characters are hierarchical: those occurring earlier in phylogeny ("more primitive") are more general and include phyletically younger, less general ("advanced") characters. This property is true regardless of the direction of any ontogenetic transformation, as demonstrated by the occurrence and recognition of fetal

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specializations. (Nelson's version of the biogenetic law is equivalent to: given an ontogenetic character transformation, from a character observed to be primitive (more general) to a charcter observed to be advanced (less general), the more primitive character is primitive and the advanced advanced. The independent clause is true by definition, regardless of the content of the first clause. Ontogeny is a source of evidence for polarity not because of transformations, but because it provides more forms over which to determine the generality of each character state's distribution and therefore enable determination of whether that state is primitive or derived relative to related states.

Character transformation in ontogeny can provide additional information. Just as in step 1 (Figure 15), in which similar ontogenies were considered corroboration (and dissimilar ontogenies contradiction) of the hypothesis that the character states in two taxa were the same, similarly in step 2, the transformation in taxon X of a character state resembling more closely the adult condition in taxon Y from or into a different state in X implies that those two character states are closely related (they certainly share similar ontogenetic development) and should be linked in a transformation series, although direction of that series is not indicated. This might have been Nelson's (1973) point

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since he explicitly disavowed acceptance of a recapitulation argument. However, in his example and discussion here and later (1978; Nelson and Platnick, 1981), the direction of the transformation was accorded significance. To argue that the direction of transformation parallels the direction of phylogeny constitutes an additional assumption (Wiley 1981: 154), one discussed extensively by Gould (1977) and shown to be certainly not without exception.

If one were willing to make the assumption that more closely related taxa have very similar ontogenetic stages for a longer span of their ontogeny, then one could use that as an interpretive theory to argue that two features that have a greater number of similar early ontogenetic stages are to be more closely linked in a character state tree, and that a feature with fewer similar stages is relatively primitive. Again I decline to adopt such an assumption: the interaction between phylogeny and differentiation seems to me entirely too complex and diverse to make such a simplistic assumption very reliable without a great deal more critical analysis than is provided here. And in both this case and the one in the preceeding paragraph, sufficiently detailed ontogenetic information is so rare for extinct taxa, and even most relevant extant taxa, that such an assumption would not be productive for the present study.

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In very general terms, however, the criterion of distribution of character states throughout ontogenies often provides evidence for polarity as described above. Interestingly, the first criterion, that of novelty or restricted distribution, can be considered a special case of the ontogenetic criterion, and if one does so, it is by far the most common situation: if in Figure 17A, character state a1 is the absence of a feature and a2 its presence, the ontogenetic sequence shown is almost always observed. Almost all adult features are completely absent in early embryonic stages. "Absence" is the most general and universally primitive character state.

Teratology provides a final bit of ontogenetic evidence for polarity. As Stevens (1980) noted, developmental abnormalities surprisingly often appear similar to character states seen in other taxa. This phenomenon is generally interpreted to be the result of the aberrant expression of some quiescent gene sequences representing the primitive condition. Whatever the genetic basis, the important thing to be noted here is that the occurrence of a character state in a taxon in which it is not usually seen increases the relative generality of that state's distribution, and on that basis alone should be identified as the primitive condition.

A third criterion may be derived from our assumptions that phylogeny occurred, accompanied by character

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transformation, by recognizing that primitive character states must be absolutely older than relatively derived states. Stratigraphic position gives us the relative age of the first observed occurrence of each character state. (Almost all previous discussions of stratigraphic sequence have unnecessarily and unfortunately added some qualification, such as "within the lineage", that implies some a priori knowledge of the phylogeny. Such qualifications would remove this criterion from usefulness in character analysis. It is only necessary that the character states are homologous such that the question of polarity makes sense.)

As with the first two criteria, it is possible to decide that mistakes have been made, as shown by ad hoc hypotheses, but that possibility alone of course does not negate the potential utility of stratigraphic sequence as evidence for polarity. As with any criterion for polarity, or indeed any subsequent stage in phylogenetic analysis, erroneous conclusions can arise from mistakes in our hypotheses of homology (results of step 1) or from mistakes or gaps in our distributional data (what animals possess the character state at what point in their ontogeny, and in this case, what are the geologic ages of those animals). The pertinent question in this case is the expected frequency of mistakes. One of the assumptions behind the morphological analysis is that we

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obtain the right answer often enough to be able to pull the signal (phylogenetic relationships) out of the noise (misidentifications, convergences, reversals, neoteny). An equivalent assumption for polarities inferred from stratigraphic sequence is much less sound: as has often been noted, the fossil record varies widely in its completeness, and can be quite misleading, as has been occasionally demonstrated by surprising range extensions for some taxa.

Our risk of error must vary widely if this apparently great variation in completeness is true (see review by Raup, 1979). Confounding the problem is the realization that we have no very direct evidence about the magnitude of our risk of error in any given case, so we cannot easily judge when it is reasonable to use stratigraphic sequence as evidence of polarity and when not. While not deciding in despair or for socio-political reasons to ignore paleontological evidence altogether, I do give higher priority in cases of conflicting evidence to novelty and ontogeny as indicators of polarity, and would in any case use stratigraphic sequence only when the record appears to me dense enough to reduce the likelihood of incorrect conclusions. Such a conservative approach is based on my judgment of the soundness of the assumptions about the frequency of mistakes in the 'empirical observations' relative to this level of analysis; this

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criterion is still as logically valid as novelty or ontogeny, both of which require parallel assumptions.

One point is important to reiterate because of its deviance from the current systematic literature: the evidence is the relative ages of first occurrence of the character states in question, without regard to the group membership of the taxa involved. Of course, something about group membership is implied, in that the two character states must be thought homologous, which then implies that there is some character that includes those two character states, and some group, all of whose members possess that character in some form, including the taxa bearing the two character states in question. But the overall distribution of that character need not be known, nor the group recognized. And certainly there is no ancestral-descendant relationship implied: the taxa bearing the character states in question do not have to belong to the same "lineage" (contra Kluge, 1977, for example). Nor does a criterion of stratigraphic precedence imply that, if animal X is older than animal Y, all of X's character states are primitive relative to Y's: the evidence is the sequence of first occurrence of the character states, not of taxa. Animal Y may share some character states with animals older than X while some of the corresponding conditions in X might be relatively derived.

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Other criteria for determining polarity.--Recent reviews have summarized a remarkable number of criteria for deciding the polarity of a pair or series of character states (e.g., Arnold, 1981; Crisci and Stuessy, 1980; de Jong, 1980; Marx and Rabb, 1970; Stevens, 1980). Since some of these criteria appear to be widely accepted, it may be useful to explain my rejection of them.

The three criteria discussed in the previous section follow logically from the assumptions outlined on pp. 39 to 41: if those assumptions are true, then these criteria are always valid. The only source of error will be in our ability to recognize the homologies of the various character states, most importantly the ability to distinguish between loss and absence of a feature, and in the completeness of our information. But if our assumptions are true (and to my knowledge they have not yet been refuted elsewhere), if we could recognize all homologies correctly, and if our information were complete, then the polarity indicated by any of the tree criteria must be true.

In contrast, the best of the other criteria proposed in reviews require additional assumptions, usually about specifics of the mechanics of evolution. Furthermore, even if all assumptions are true and our information complete and accurate, the polarity indicated by these criteria is at best only likely to be true. It is always

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possible under such criteria that we could continue to test and corroborate our assumptions and evidence, gather more and more evidence, and still be flatly wrong in our conclusion with no means of discovering the error except by recourse to other criteria.

Out-group comparison has a status different from that of the three criteria in character analysis, in that it requires for each application the assumption of a specific phylogeny: the monophyly of the group under study must be assumed. Thus out-group comparison is ontologically part of cladistic analysis and not character analysis. The use of this criterion presupposes, even if by a long regress, the application at some point of some other criterion to establish the characters used to recognize the initial monophyletic group. Novelty and restricted distribution constitute the criteria most often used to establish the initial monophyly of the group within which the phylogenetic relationships are to be determined, after which out-group comparison maximizes the parsimony of the remaining character hypotheses within the context of a now assumed monophyly.

Several criteria that have been repeatedly proposed are logically invalid. For example, various forms of a "commonality" principle have been proposed. Sometimes out-group comparison is meant. Sometimes the criterion states that the most common character state within the

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group under study is primitive. This version is easily shown to be invalid: there is nothing to preclude, for example a one-state character defining a group comprising the vast majority of the taxa, and the remaining few taxa possessing the homologous primitive character state. Some authors have tried to redefine what is meant by most common to avoid such situations: Kluge (1976: 22), for example, emphasizes that "a character state should be considered widespread only when it is exhibited by several taxa that otherwise have little in common." This will still not be invariably true (mistakes in homology aside) since in reality nothing precludes the primitive character state being retained by only one species or one monophyletic group in the entire group under study. A potential source of confusion can be avoided if it is kept in mind that the relatively primitive character is the more generally distributed because it comprises the most primitive character state (which may be rare or common) and all derived character states (all modifications of that character).

There is also the strong flavor in Kluge's version of an a priori phylogeny: even if "several taxa" is interpreted to mean the smallest units being studied, "otherwise have little in common" implies more distantly related taxa within the group, a judgment that is to be the result of the analysis, not an assumption. Arguing

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from the opposite direction, Estabrook (1977) points out that while "common is primitive" may not necessarily be evolutionarily correct, employment of that criterion will help minimize the number of convergences and reversals required by the best-fitting cladogram in cladistic analysis, and therefore might be preferred in order to maximize parsimony at that higher level of analysis. This reasoning, which also removes the criterion from character analysis to cladistic analysis, will be discussed below (pp. 108ff).

Another form of a correlation criterion is the idea that primitive states are more likely to co-occur (e.g., Arnold, 1981; Crisci and Stuessy, 1980), for which expectation I can find no logical basis whatsoever, at the level of character analysis. A related concept is the idea of a "primitive taxon" (rampant in Crisci and Stuessy, 1980; clearly implied in Kluge and Farris, 1969, and Kluge, 1976). One need only consider that even a species that is the sister group of all other taxa in the study may fairly reek with autapomorphies to see that a concept of a "primitive species" is a misleading one.

Numerous other criteria have been proposed, most of which are satisfactorily shown inadequate by de Jong (1980). Of the seven criteria that de Jong accepts, one is out-group comparison, one is a version of a criterion of geological precedence, and the remaining five all

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require unrealistic assumptions or unobtainable data or both. We are left with three valid criteria, novelty, ontogeny, and paleontology, in character analysis, and one criterion, out-group comparison, in cladistic analysis.

Ad hoc hypotheses.--Conflict among various pieces of evidence and the resulting anomalies that contradict the current hypothesis are explained by ad hoc hypotheses. These hypotheses do not add to the information content of the hypothesis they are protecting, nor do they refute the anomalous empirical observations. Ad hoc hypotheses should always be minimized in order to maximize the parsimony or explanatory power of the current hypothesis, but cannot be entirely avoided (contra Ghiselin's (1980) wishes). As mentioned earlier, there are nearly always anomalous, contradictory data relative to even the best hypothesis; our goal continues to be a hypothesis that accounts for as much of the relevant data as possible. Various ad hoc hypotheses are used at different stages in phylogenetic analysis.

Table 4 summarizes the steps in character and cladistic analyses, and the ad hoc hypotheses that may be invoked at each step. Contradictions may arise, for example, among the various 'empirical observations' used to construct and evaluate various hypotheses of the form 'feature X in taxon A is the same as feature X in taxon B'. Numerous categories of ad hoc explanations supply

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possible explanations of such anomalies. For example, the elongate condition of the ulna of horse A is homologous with the elongate condition of horse B, compared with the ulna of a rhinoceros, in spite of (and here is the ad hoc hypothesis) the individual variation reflected in A's ulna (thoroughbred) actually being proportionately longer than B's ulna (Clydesdale).

All ad hoc hypotheses in this category argue basically that morphology that apparently contradicts the hypothesis of 'sameness' either is not a critical anomaly (due to individual variation) or is not what it appears to be (due to breakage rather than the real morphology, or due to environmental influence rather than a heritable feature significant in our analysis). In other words, these ad hoc hypotheses deny the truth of some information from level I--morphology. Most if not all of the ad hoc hypotheses at step 1, as well as the application of the interpretive theories (such as those used to decide what is likely to be heritable or not, etc.) appear to me to be testable. For example, breeding experiments and raising of the offspring in controlled environments would demonstrate if the condition of some feature is environmentally induced or not. Such ad hoc hypotheses are employed to deal with contradictions until the point is reached that the investigator decides that it is more parsimonious to revise the initial hypothesis. Clearly,

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the degree to which the ad hoc hypotheses are themselves corroborated would affect how soon such a point is reached.

At step 2, the forms of the ad hoc hypotheses are less numerous, and there is a strong bias in favor of one over the others. Contradictory evidence for the relative primitiveness of character states may come from the three criteria advocated here (Figure 15). If the fossil record disagrees with either of the other two, the ad hoc hypothesis is almost always "incompleteness of the fossil record".

The result is not so certain in those rarer cases in which ontogeny and novelty disagree. In the case of whales, for example, the baleen whales lack teeth as adults while the odontocetes have teeth. The criterion of novelty would dictate that absence is the general state and presence the derived. But ontogenetic information demonstrates the relative generality of teeth in the mysticetes: teeth develop briefly and are subsequently resorbed. So we accept an ad hoc hypothesis, relative to the distribution across the adult morphologies, that what looks like the universal primitive condition "absence" in mysticetes is really "loss", a derived condition.

A simplistic contrasting example may be found in the relative brain size in the great apes, and especially humans, versus other chordates: the novelty criterion

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dictates the absence of cephalization would be primitive, and combined with the classic transformationist model (see p. 116), the other end of the spectrum, exemplified by the large hominid brain relative to body weight, must be derived. However, when one looks at chordate embryos, early fetuses have proportionately very large brains for their body size. In contrast to the previous example, rather than postulate the loss of large brain size in other chordates, biologists typically invoke an ad hoc hypothesis of neoteny: the human condition is a derived retention of an embryonic condition.

Both neoteny and loss are much rarer ad hoc hypotheses at this stage than is the incompleteness of the fossil record. This is doubtless in large measure due to the observation that the criteria of restricted distribution in adult forms and generality of distribution in ontogenetic stages produce congruent results in the vast majority of cases.

All ad hoc hypotheses at this step explain away some contradiction in the distribution of character states, information from level II (Figure 15). I find it more difficult to conceive of a test pertinent to the ad hoc hypotheses in this category.

Although the third step is cladistic analysis, the ad hoc hypotheses invoked by cladistic analysis are appropriately discussed in this section because they

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explain anomalies in the evidence from character analysis. The ad hoc hypotheses produced under cladistic analysis fall into two categories: those that re-interpret information at level II and those that re-interpret information at level III. As described above, an anomalous distribution over the stratigraphic column is explained by an incomplete fossil record. An anomalous distribution over ontogenetic stages is explained as neoteny.

Since these were both ad hoc hypotheses in character analysis as well, it may be useful to give an example illustrating the difference between invoking neoteny, for example, from character analysis and from cladistic analysis. Table 5 compares the examples described above with a third case in which the criterion of restricted distribution (novelty) gave a result at variance with the criterion of generality of distribution over ontogenetic stages. In the first type of case, evidence from ontogeny is usually given precedence. In the second case, the factor that might be considered tc give novelty in the adult stage greater weight is a transformationist argument that identifies lack of cephalization as primitive and a small brain as an intermediate step.

Example C outlines a third case for which there is no very conclusive argument one way cr another, and given ontogeny's usual edge, would probably result in an ad hoc

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hypothesis of loss of gills being derived for other urodeles. Cladistic analysis, however, results in a hypothesis of relationship and comcomittant character transformation that requires that no gills in the adult be the primitive condition and that retaining gills intc the adult stage be a relatively derived condition--neoteny. Just as in the previous example, neoteny is an ad hoc hypothesis used to explain away the contradiction that the distribution of character states over ontogeny presents to the current hypothesis, in this case, the cladistic hypothesis as well as the character hypothesis.

Thus some contradictions among character hypotheses that become apparent in cladistic analysis can be explained by ad hoc hypotheses rejecting the apparent distribution of character states implied by the sources of evidence at step 1. Cther contradictions may be dealt with by arguing that what appeared to be one character state with a given distribution is really two exclusive character states with part of the distributicn respectively--i.e., convergence--or two nested characters, one more generally distributed and the other an included derived condition--i.e., reversal. Again, these ad hoc hypotheses argue for different distributions than were hypothesized on the basis of the criginal evidence from character analysis.

Neither convergence nor reversal is a particularly

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strong hypothesis, in that neither are strongly testable. Both types of hypothesis are of the form: "feature X is not the same as feature Y". Only negative evidence--the failure to find differences--will contradict it. The significance of this observation is discussed further in the next section.

A frequent plea is made to identify convergence (or parallelism) before the cladistic analysis (e.g., Hecht and Edwards, 1977; Bock, 1977; Ghiselin, 1980), a plea that reflects another very different meaning of the term(s). Convergence, in the sense used in this study, is a mistaken hypothesis of identity between the character states in two taxa (a mistake identified of necessity a posteriori to the cladistic analysis). If character analysis did not produce a hypothesis that the character states were the same, one would not have made the mistake and there would be no reason to call the states convergent. The other sense of the word "convergence" connotes some sort of non-homologous similarity, of interest perhaps in functional or adaptational arguments, but not relevant to the construction of phylogenetic hypotheses. Of course our goal is to identify homologies and delineate characters accurately in character analysis and prior to the cladistic analysis. Restriction of the term "convergence" to those mistakes identified ad hoc gives it a very precise meaning; "analogous" is available

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for a priori non-homologous similarity. Use of these terms in this precise fashion in no way reflects the amount of or lack of zeal or correctness with which one does character analysis.

Another term for which various meanings have been proposed is "parallelism". I have not found this a particularly useful term. Wiley (1981) defines parallelism as the independent origin of indistinguishably similar characters from the same ancestral character state. Convergence is the same but from different (dissimilar?) ancestral character states. (He must mean "dissimilar" because the convergent character states are different (not evolutionarily "the same") although similar, and if "dissimilar" were not meant, the distinction between parallelism and convergence would reflect merely the number of character states we recognized in the two lineages between the change from the common ancestral condition and the states being labelled.) Since these definitions require a cladogram and recognition of (hypothetical) ancestral states, such identification of parallelism and convergence must succeed the cladistic analysis. In any case, I have not discovered a use for the distinction and here use "convergence" for both conditions.

Several definitions of parallelism (e.g., Simpson, 1961; Hecht and Edwards, 1977) involve the inheritance

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from a common ancestor of a genetic or embryological tendency to develop the feature so that when it develops it is very similar in the two descendants. If there are no intervening descendants lacking expression of the feature, the feature is a true indicator of relationship, can be treated as such for the purposes of hypothesizing a phylogeny, and indeed cannot be distinguished from a normal character unless the ancestor is known. Then the question arises, how does one know that that is the common ancestor, since it does not possess all the features common to all its descendants?

If there are intervening descendants lacking the feature, they must have lost the tendency to develop it (one ad hoc hypothesis) which is equivalent from our perspective to the single ad hoc hypothesis of convergence (which does not require the additional unlikely supposition that we know something about the genetic tendencies of an unknown ancestor). In either case, the occurrence of intervening descendants can only be demonstrated by a cladistic hypothesis, so distinguishing between these two situations is an ad hoc procedure. None of the references supply criteria by which to recognize the genetic or embryological tendencies of unknown ancestors prior to or even after the cladistic analysis.

Therefore, in summary, I find the instances of parallelism under some definitions indistinguishable from

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informative character distributions, and under other definitions, indistinguishable from convergence. Convergence can only be identified after the cladistic analysis, as an ad hoc identification of mistakes in character analysis. Character states demonstrated to be different in character analysis are not informative at that level for phylogenetic analysis (although their homologies may certainly be informative).

Ad hoc hypotheses in cladistic analysis may also be aimed at the information or hypotheses at level III. Some contradictions among character hypotheses can be explained by postulating an error in the topology of a character state tree (III) rather than in the distribution (definition) of character states (II). Two such ad hoc hypotheses are possible: either the polarity of a two-state character state set is reversed, or the relative ordering of states in a transition series of three or more states is altered. To do either, however, causes a conflict, because the evidence from level II that supported the original polarity or ordering is not explained. This problem can be analyzed in terms of the level(s) of analysis at which parsimony is being maximized. Such an analysis is presented in the next section.

"Testing hypotheses of homology" with phylogenies.--Recognition and formalization of character

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analysis as a separate level of analysis permits a more complete consideration of arguments of relative parsimony and the different levels of hypothesis testing. In those few discussions of cladistic analysis in which a statement of homology (i.e., step 2 in the scheme in Figure 15) is recognized as a hypothesis rather than an observation, this hypothesis of homology is said to be tested by the phylogeny derived from it and other relevant hypotheses of homology. The lower-level hypotheses, the 'empirical observations' relative to the current level of analysis, are considered tested by the very higher-level hypotheses derived from and tested by them in the first place. This has been labelled "reciprocal illumination" (e.g., Wiley 1981: 139). Before discussing the logical problems with this procedure in the abstract, let us survey the various specific possibilities in phylogenetic analysis.

As was shcwn in the discussion of Wagner trees and networks above (pp. 46ff), it is possible to root a network by designating an out-group, or on the basis of a few novel characters, and to derive from the resulting tree the most congruent hypotheses of polarity for the remaining transition series (also noted in Estabrook, 1972). The polarities of these transition series wculd then be the result, not of character analysis, but of a process of maximizing the apparent parsimony at the tree or cladogram level--maximizing the congruence among

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transition series. And, of course, characters whose polarities are derived directly from a hypothesis of phylogeny cannot be used to corroborate or contradict any hypothesis of phylogeny, since they will autcmatically be most congruent with the phylogeny from which they are derived (see Figure 18). Therefore, transition series without some order and direction hypothesized prior to the cladistic analysis are not useful in cladistic analysis: they are not relevant to deriving or testing a hypothesis of phylogeny. Order and direction can be specified for each set of character states on the basis of evidence from any of the sources listed in Figure 15, or they can be implicitly decided for each set of character states within a given set of taxa by specifying one or more additional taxa as out-groups. (This latter case is equivalent to taking a larger phylogeny as given, and in that context finding the most parsimonious character state trees in the more local phylogeny.) But there must be some outside source of information about the relative generality of the various characters, outside the hypothesis of phylogeny being derived or tested.

If we now consider only those sets of character states for which character analysis has suggested some order and direction--i.e., for which we have a character state tree--we find that incongruences can be dealt with in two ways. One way, the most common, is tc use the

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fewest possible ad hoc hypotheses of convergence or reversal to account for the incongruence. Either convergence or reversal is an ad hoc hypothesis of mistaken identity (a mistake at step 1 in the scheme in Figure 15): under our assumptions about evolution, incongruences mean that the condition of some feature in two taxa was mistakenly thought to be the same character state, but must have been instead evolved independently. In the case of convergence, two seemingly indistinguishable character states are independently evolved from some ancestral condition(s) (I will not bother with a distinction between parallelism and convergence), whereas a reversal is the evolution later in a tree of a character state indistinguishable from one occurring earlier.

As ad hoc hypotheses, both convergence and reversal are identified after the tree is derived; they are not and cannot be the product of character analysis. And they are not themselves particularly testable hypotheses: both are hypothesizing that two similar conditions are actually more different than first thought. Any differences subsequently found corroborate this idea, but the only sort of evidence that can contradict it is negative evidence--the failure to find any differences. (Because convergence and reversal are only weakly testable if at all, it is more useful in cladistic analysis to retain

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them in the hypothesis as convergences or reversals than to recode them to agree with the current cladogram. They consititute anomalies that may be important in supporting an alternate hypothesis of phylogeny, but would be difficult to recognize as such if recoded to appear congruent with the very cladogram with which they are anomalous. Recoding is counter-productive in the context of methodological falsificationism.)

The second possible response to incongruences is to consider the polarity or order of incongruent transition series to have been refuted by the most parsimonious cladogram. Rather than considering incongruence an anomaly to be resolved by ad hoc hypotheses of convergence or reversal, the hypothesis of polarity is considered refuted by the contradictory phylogeny and the direction of the transition series or part of the series reversed.

Examples will clarify this. In Figure 19, a hypothetical data set illustrates how reversing an initial overall hypothesis of polarity for a transition series can produce a tree with apparently fewer steps. Such a shorter tree is more parsimonious at the level of cladistic analysis because it requires fewer (in this case, zero) ad hoc assumptions of convergence or reversal for the characters as newly defined.

This reasoning has recently been taken to its next logical step: incongruences among characters can occur in

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Wagner networks, and are in such cases not the result of conflicts among the overall polarities of transition series (e.g. c3 --> c2 --> c1 versus c1 --> c2 --> c3) but the result of conflicts among relative polarities within the series--the ordering of the states. (The other possible simple linkages for three states would be c1 <--> c3 <--> c2 and c2 <--> c1 <--> c3.) Mickevich has devised a method (partially described in Mickevich, 1981) to produce the maximally congruent ordering for all the transition series in a data set, thus maximizing even further the cladistic parsimony of the hypothesis represented by the final cladogram. Figure 20 illustrates the re-ordering of one incongruent transition series.

In both examples, the parsimony of the cladistic hypothesis has been maximized. But in both cases, parsimony at the cladistic level has been maximized at the expense of parsimony at the character analysis level, with a resulting loss of overall parsimony. This can be seen by reanalyzing both examples with the results of the character analyses made explicit.

Character state trees are suggested by character analysis, that is, order and direction are assigned to each transition series, if evidence is found that refutes all possible trees save one, i.e., that contradicts one the least. Character analysis produces the tree a1 --> a2 --> a3 if evidence is found that an organism possessing

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state a2 really had a special attribute a2 added on to or modified from a more generally distributed state a1. Such evidence might be ontogenetic, for example, if a2 were observed to develop from a1 within an organism's ontogeny. Thus we may note more accurately the character state possessed by such an organism to be (a1)a2. Similarly, a3 could be ordered in the transition series if it were observed that organisms with character state a3 also possessed a2 earlier in ontogeny. And state a3 would be more accurately designated ((a1)a2)a3.

At this point it might be noted that the hierarchic nature of characters devolves nicely from this notation. The distribution of character A1 is the complete distribution of character state a1. State a1 is common to organisms with states a1, a2, or a3: a1, (a1)a2, and ((a1)a2)a3 respectively. Similarly, the distribution of character A2 is shown by the occurrence of state a2 in organisms with a2 or a3: (a1)a2, or ((a1)a2)a3. And character A3 is restricted to only those organisms with state a3: ((a1)a2)a3. The distribution of A2 is thus included within that of A1, and A3 in both A2 and A1: the character state tree a1 --> a2 --> a3 implies the hierarchy or nesting of characters A1(A2(A3)), equivalent to a phylogenetic hypothesis for the taxa possessing those characters.

Given the distributions of the character states, we

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can now evaluate the relative parsimony of alternative character state trees at the level of character analysis. If we observe (a1)a2 in organisms with state a2, then a1 is more general and therefore primitive. Thus, as was stated earlier, character analysis, given the distributions of character states a1, a2, and a3 described above, would produce a1 --> a2 --> a3 as the most parsimonious character state tree. Any other tree would require ad hoc hypotheses of additional gain or loss of character states to explain the distributions discovered in character analysis.

Returning to the example in Figure 19, it is clear that the 'shorter' tree obtained by reversing the polarity of the series c1 --> c2 --> c3 to c3 --> c2 --> c1 is only shorter in a cladistic analysis that considers each possible transition equally parsimonious and ignores the evidence of the relative generality of the character states. If there were evidence from character analysis supporting c1 --> c2 --> c3, it must have been evidence demonstrating that c1 was the more general state and c3 the least. Therefore, the revised character state tree c3 --> c2 --> c1 really requires four steps if the information from character analysis is considered. Similarly, in the example in Figure 20, changing the order of the states also results in a less parsimonious tree in the context of the information from character analysis.

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These examples demonstrate that some ad hoc hypotheses used to increase the apparent parsimony of a specific cladistic hypothesis will generate additional anomalies relative to the evidence that produced the original character analysis. Attempts to maximize the parsimony of a hypothesis at just the cladistic level thus run a risk of costing more in loss of parsimony at the character analysis level than is gained at the cladistic level. Such procedures also increase the invulnerability of a cladogram to refutation: convergences and reversals are still relatively recognizable as incongruences that contradict the current hypothesis (as long as they are not recoded to appear congruent) and may add their weight to additional contradictions, but re-ordered or redirected transition series no longer contradict the current cladistic hypothesis, even though the evidence for the original transformation series is as anomalous as ever relative to the cladogram. The lower-level hypothesis that served as the initial 'empirical observation'--the original character state tree--has been abandoned although not directly refuted.

Of course, for those characters for which we have no evidence about the ordering or direction of a transition series from character analysis, determining the most parsimonious polarity from rooting a Wagner network (equivalent to the correlation criterion--see criterion 6

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in de Jong, 1980) or the most parsimonious ordering from Mickevich's transition series analysis cannot generate additional anomalies. However, it is important, although it may be difficult, to remember that the polarity or order of transition series so directed or ordered cannot be counted as support for any specific cladogram, since these series are directed or ordered specifically to agree with the current cladogram and not on the basis of any independent evidence or 'empirical observations'. Indeed, even mere congruence is not very strong support since it is much more difficult for an unordered, unlinked set of character states to contradict a network. Sets of character states for which character analysis has not suggested polarity or order are not nearly as informative at the cladistic level as are sets of character states for which a character state tree has been corroborated.

The above argument about relative parsimony is clear cut for those character state trees whose topology was based on pertinent ontogenetic information or for those 'two-state' trees in which one state is merely the absence of the feature constituting the other state. Ambiguity arises when the incongruent character state tree was ordered or directed on the basis of other sorts of evidence. If we derive the level of generality of a character from some indirect criterion, i.e. other than directly observing the more general character state

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preceding or accompanying more derived states, we are still inferring that the more general condition is part of or preceeds the more specific. But the strength of this inference may be questioned.

For example, let us consider a transformation series d1 --> d2, for the polarity of which our sole source of evidence is the earlier occurrence of d1 in the fossil record. We have inferred from d1's apparent relatively greater age that d1 is more general and that d2 the more specific, i.e., that d1 --> d2, that d2 is actually part of d1: (d1)d2. If the cladogram based on this and additional transformation series is incongruent with d1 --> d2, we have the ad hoc hypotheses of convergence and reversal available to explain the observed character state distributions. However, since the relative generality of the states was an inference rather than a direct observation, we can question the validity of the interpretive theory behind our inference: we thus have resource to the ad hoc hypothesis that our conclusion was incorrect because the fossil record is incomplete, and that the transformation series is actually d2 --> d1. This must be considered an ad hoc hypothesis because the anomaly still exists: our lower-level hypotheses, our 'empirical observations' (step 2 in Figure 15: relative ages in the fossil record), still support the hypothesis (character state tree) d1 --> d2. This has not been

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refuted: it has not been replaced by an alternative hypothesis that better accounts for more 'empirical observations', only by one that agrees better with still higher-level hypotheses.

Although Nelson and Platnick's (1981) discussion of what they term the paleontological argument seems to present the choice between two ad hoc hypotheses as a drawback, in reality it matters little as long as one remembers that ad hoc hypotheses represent unproductive explanations of anomalies relative to the current cladistic hypothesis, anomalies that argue for an alternative hypothesis. It is the existence of those anomalies and the degree of support for an alternative hypothesis that are important, not which ad hoc hypothesis is chosen. (Nelson and Platnick's repeated references to the possibility of "falsifying the paleontological argument" itself are not a useful consideration: methods themselves are not "falsifiable" hypotheses within the system. Some assumptions upon which a method is based or the interpretive theories used in evaluating evidence could be refuted in an outside, higher-level analysis, or the logic of the method could be shown to be faulty and the method shown thereby to be invalid, but the method cannot reasonably be said to be refuted in the same way that a hypothesis is refuted.)

Usually criteria for the overall direction or

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polarity of a transition series are considered to the exclusion of the determination of the ordering within series comprising more than two states (e.g. de Jong, 1980; Crisci and Stuessy, 1980). The most common procedure, rarely stated explicitly, appears to have been to order the states on the basis of what seems somehow inherently logical. Kluge (1976: 10) describes it thus: "The sequencing in the other patterns is based on the assumption that the most evenly graded series of changes is the evolutionarily-most-probable hypothesis (Fisher, 1958: 41-4)." For example, if the mastoid process is present in different taxa in two states, one (a1) small and the other (a3) large and elongate, the assumption has been that a third state, a moderately sized, slightly elongate mastoid process, in a third taxon, is an intermediate condition. In current practice, attention immediately shifts to determining (hypothesizing) which extreme is primitive. However, the number of character state trees to be considered has been greatly reduced by this decision, as shown in Figure 21.

Such an assumption is an example of the influence on systematic methodology of the often unquesticned acceptance of specific ideas about evolutionary processes. The inherent reasonableness of this logic about the character state tree depends on a transformationist model of gradual and ordered change in morphology throughout the

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phylogeny. (Whether the time span over which this smooth continuous change takes place is (relative tc the length of time that the species exist) lcng, such as in a phyletic gradualism model of phylogeny, or short, as in a punctuated equilibrium model, is irrelevant to this discussion of the order of character states.)

Of course, at the level of the individual, discontinuity exists perforce. But systematists try to define character states so that they are attributes common to the individuals within taxa, attributes of populations, and therefore embracing some range of variation within each state. The transformationist model postulates that the ranges of variation in succeeding generations overlapped, so that one state would have transformed continuously (whether quickly or slowly) intc another during phylogeny. Some systematists thought they knew when a character state represented "a structural configuration through which other character states developmentally or evolutionarily must pass" (Smith and Koehn, 1971: 286). Under such a model, recognition of a character state as <u>intermediate</u> automatically dictates a restricted class of character state trees--those whose general network has the intermediate state linking the other two (Figure 21A).

If the subsequently derived phylogeny is incongruent with all three possible character state trees for this

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network, then we have recourse to the ad hoc hypotheses of convergence or reversal, or, if the most parsimonious phylogeny has been derived using Mickevich's transition series analysis, the ad hoc hypothesis that the ordering of the character states was incorrect. In this case, the relative generality of the various character states was not observed directly. Indeed a1--> a2 --> a3, a3 --> a2 --> a1, and a1 <-- a2 --> a3 are all congruent with the same Mickevich network (Figure 21A) but all imply very different generalities and characters: a1 --> (a1)a2 --> ((a1)a2)a3, a3 --> (a3)a2 --> ((a3)a2)a1, and (a2)a1 <-- a2 --> (a2)a3, respectively.

So is there a loss of parsimony at the character analysis level (i.e., as there was in the example in Figure 20 above) if the transition series is re-ordered in a Mickevich transition series analysis? There is a loss of parsimony only if the reasoning that produced the ordering a1--a2--a3 is considered valid: if the revised hypothesis for this set of character states produces a tree corresponding to a different Mickevich network, a1--a3--a3 or a2--a1--a3, the evolutionary distance from a1 to a3 must still be twice that from a2 to a1 or a3 if a2 is truly intermediate. The networks would actually be a1--a2--a3--a2' and a2'--a1--a2--a3 respectively, and the trees correspondingly a step longer than any for the original Mickevich network. So the next question is: is

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the reasoning that a2 must be intermediate valid? That is, is the transformationist model one we want to adopt as an assumption?

What I have dubbed here the transformationist model was, until recently, nearly universally accepted. Simpson's (1953) discussion is almost entirely an elaboration of this basic model, for example. Recently, however, assumptions about what is 'known' about evolutionary processes have been questioned by a revival of interest in macroevolutionary processes (in contrast to the microevolutionary process of change in gene frequency and an accompanying gradual change in the morphologies observed within a population). A variety of processes have been proposed that might result in the abrupt appearance of a new morphological condition (see Dover, 1982a and 1982b, for example). Albercht's (1980; Albercht, et al., 1979) hypotheses in particular suggest that apparently abrupt change could be change that merely appears morphologically far from the original but is actually very close in developmental distance: "continuous perturbations in the parameters controlling timing and rates of development can result in major discontinuities in the final morphological outcome." (Albercht 1980: 662-3)

In the light of these alternative models (which could be generally labelled disjunction models in contrast to

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the transformationist model), the argument that morphologically intermediate states must also be evolutionarily intermediate becomes much less compelling. Indeed, the entire practice of counting "evolutionary steps" and measuring evolutionary or morphological distances appears arbitrary and potentially far removed from any biological reality (ontogenetic or phylogenetic). (The paucity of information about either genetic and ontogenetic bases of alternative character states or the degree of difficulty of change between character states also leads me to question whether we can choose between assumptions that characters are or should be counted as roughly equal units when we decide the degree of support for alternative hypotheses and any possible weighting schemes based on our present ignorance. See pages 29 and 53.)

Early 'rules' or 'laws' about possible evolutionary changes, such as Cope's rule or Dollo's law, have been generally recognized as subject to exceptions, but the likelihood of exceptions has probably continued to be underestimated in some cases. For example, the widespread assumption that complex structures or systems cannot be regained after being lost has been disproven by several demonstrations of the apparent retention of the genetic basis for such complex structures (e.g., Jannett, 1975), in some cases over a very long time interval (e.g., Kollar

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and Fisher, 1980).

I fail to detect unanimity among the various kinds of evidence for either the transformationist or disjunction models. I expect that unanimity will never be obtained because both models are probably valid under specific circumstances; the problem is to determine those circumstances. The present choice between the two models does mean that there are respectable theoretical grounds from which to question the applicability of the transformationist model to a given character state tree. Therefore, there is no clear theoretical reason to argue that the re-ordering of states as a result of a Mickevich transformation series analysis necessarily implies a loss of parsimony at the character analysis level if the series was initially ordered under the transformationist model. An alternative ad hoc hypothesis is available: this transformation series is one that is better interpreted under the disjunction model. (Of course, re-ordering under a Mickevich analysis does still, as shown earlier, result in an overall loss of parsimony if the initial hypotheses of polarity and order were deduced from from direct observation of the generality of distribution of the various character states, rather than by inference from relative age or the transformationist model.)

Estabrook (1977) has used a maximum parsimony argument in support of a polarity criterion that

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identifies the most common character state as primitive. As shown earlier, this criterion is not a logical conclusion, neither from our present assumptions nor from any assumptions directly that we might want to adopt. But one may ask what merit there is in the rationale behind this criterion and Mickevich's transformation series analysis--the rationale that quite correctly points out that our assumptions about evolution require that true character hypotheses be congruent with each other, and argues that majority rule is all we can follow. Can phylogenetic analysis be done without character analysis? At the most trivial level, no: step 1 in character analysis is still necessary to define the sets of character states that will be ordered in the analysis. If no information whatsoever pertinent to step 2 (Figure 15) is available, then the "common equal primitive" criterion for two-state characters and Mickevich analysis for several-state characters will obviously produce the most parsimonious hypothesis. But this is true only if there are no data at step 2 at all. And in such a situation it seems obvious that a useful way to test the cladistic analysis would be to analyze the characters more thoroughly and check the correspondence of corroborated character hypotheses with the cladogram. Such a dearth of information seems to me unlikely in any case: we can hardly help but learn something about the distribution of

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a feature even while concentrating on step 1, and such evidence should not be ignored.

Let me summarize this discussion by generalizing briefly in terms of levels of hypotheses. It has been shown in each example above that the apparent parsimony of alternative hypotheses at the cladistic level may be misleading if considered in isolation, without reference to lower levels. The fundamental mistake lay in ever trying to argue that hypotheses of homology could be tested by higher-level hypotheses. 'Contradiction' of a corroborated and unrefuted character hypothesis by a cladistic hypothesis does not negate the existence of the 'empirical observations' that corroborated that character hypothesis. The character hypothesis cannot, strictly speaking, be refuted by a cladistic hypothesis (in the sense of 'refute' on page 27). The character hypothesis can only be tested by 'empirical observations', i.e., still lower-level hypotheses, and can only be refuted by being replaced by a character hypothesis that better explains more such 'empirical observations' (and which may or may not be congruent with the most parsimonious cladistic hypothesis). The unrefuted character hypothesis is itself an 'empirical observation' relative to the cladistic hypothesis--not a hypothesis to be tested but instead a lower-level hypothesis that itself tests the cladistic hypothesis. If a character hypothesis presents

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an anomaly relative to a cladistic hypothesis--that is, if a character hypothesis contradicts the cladistic hypothesis--an ad hoc hypothesis may be used to explain the anomaly, but the anomalous character hypothesis still contradicts that cladistic hypothesis and supports an alternative cladistic hypothesis. Character hypotheses can themselves be tested only by still lower-level hypotheses. Character hypotheses--hypotheses of homology--can only be tested by character analysis, not cladistic analysis.

Conclusion

Cladistic analysis has been shown in the above discussion to give a false impression of objectivity and 'falsifiability' when focussed on to the exclusion of other parts of phylogenetic analysis. A rigorous method of character analysis permits us to apply the approach so useful at the cladistic level to an evaluation of our evidence for phylogeny. We must question the identifications of features: they are not absolute facts, nor are they known 'by definition' unless they are identified on only one organism and hence useless for phylogenetic inference.

The method of character analysis outlined above is most useful when there is uncertainty or disagreement about the evidence. In such cases, this method provides a

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context in which the competing arguments and hypothese can be evaluated and tested, and more evidence sought and incorporated. Clearly in most analyses, much of the analysis at step 1 (Figure 15) does not need to be described in detail if there is no conflicting evidence. In such cases, the primary utility of the procedure is in keeping the researcher alert for the occurrence and significance of competing evidence--in other words, holding one's hypotheses lightly. When conflicting evidence does occur, character analysis provides a much needed mechanism for obtaining, evaluating, and incorporating additional information--testing the competing hypotheses.

Because the present study was of a group of extinct taxa, my formulation of this method of character analysis has emphasized morphology. This is not to deny that other intrinsic features, such as physiological attributes or behavior, can provide evidence for the phylogenetic relationships among extant taxa. Sources of evidence and interpretive theories for each step in Figure 15 could be worked out for other such sources of evidence for phylogenetic relationship.

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MORPHOLOGICAL DESCRIPTION: BACKGROUND

Introduction

The basicranium is that portion of the base of the tetrapod skull posterior to the palate. It is typically, especially in mammals, a morphologically complex region, reflecting in the bony structure the numerous blood vessels and nerves entering and exiting the skull in this region, the variety of muscle attachments (associated with increased and more precise movement of the head), and the sensory organs housed therein--the organs of balance and of hearing. Another term, "auditory region", refers to that portion of the animals's morphology, including both hard and soft tissues, associated with these two sensory organs.

Although dental morphology has historically received the most study as a source of characters for taxonomic or phylogenetic analyses (perhaps because of the much greater number of teeth well preserved in the fossil record), the basicranium was recognized by some anatomists well over a century ago to be another rich source of characters in the study of the relationships among the living Carnivora: Turner (1858) and Flower (1869) produced the first reviews of the diversity within the order. Cope (1880a) subsequently used a few basicranial characters in his studies of some fossil carnivorans, and Mivart (1881,

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1882, 1885a and b) included basicranial features in his surveys, but then the region was largely neglected for half a century until Hough's detailed analyses of carnivoran auditory regions (Hough, 1944, 1948, 1953). Although European paleontologists routinely described carnivoran basicrania, they rarely drew phylogenetic conclusions from such studies. In North America, this area was again neglected for another quarter century until R. H. Tedford and his student, R. M. Hunt, returned to the study of basicranial anatomy and its phylogenetic implications (Hunt, 1974a, 1974b, 1977; Tedford, 1976; Mitchell and Tedford, 1973; Repenning and Tedford, 1977).

Two major studies of the structure and composition of the mammalian bullae, Van Kampen's 1905 monograph, and Van der Klaauw's 1931 extension of the study to fossil mammals, surveyed the bullar portion of the auditory region, and to a lesser degree some surrounding structures, in a wide range of mammals, but discussed carnivorans only relatively briefly in the analyses. Except for these mammoth surveys, basicranial anatomy was largely ignored for all mammalian taxa for the half century between the late 1800's and World War II. However, a resurgence of interest in basicranial anatomy and its phylogenetic implications occurred earlier in the study of primates and insectivorans than in carnivorans, starting for the most part in the 1950's. As a result,

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the most complete ontogenetic information for the auditory region now available is for primates and for those groups thought to be most closely related to primates (e.g. MacPhee, 1981 and references cited therein).

In summary, then, the basicranial region of most fossil Carnivora, and indeed of many extant forms as well, remains incompletely studied. Because of the complexity of the region, it is a rich source of evidence bearing on phylogenetic relationships within the order. This report presents the results of a fresh study of the basicranial anatomy of the Oligocene and Miocene cat-like carnivorans, and considers some phylogenetic implications of those results.

General structure of the carnivoran basicranium:

Figures 22 and 23 illustrate the bones and structures in the basicranial region of a carnivoran skull. The emphasis in this description will be on the osteology, since that is what is preserved in the fossil material. Soft anatomy and ontogeny will be more briefly reviewed, because some structures are consistent enough within Mammalia to fairly safely infer their presence or condition from the bony anatomy, and because the soft anatomy and ontogeny of extant forms aids in the understanding and orientation of the osseous anatomy. The basicranial region, for our purposes, is bounded

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anteriorly by the transversely elongated glenoid fossae--the sites of articulation with the condyles of the mandible. Posteriorly, the two occipital condyles, on either side of the foramen magnum, provide the surfaces for articulation of the skull with the atlas, the first cervical vertebra.

It will be simpler to review the bones of the basicranium from the rear forward. Along the central axis, the basisphenoid and basioccipital roof the pharyngeal region. The posterior-most of these midline elements is the basioccipital, flanked on either side by the exoccipital bones. The basioccipital forms at least the posterior portion and sometimes the entire length of the medial margin of each auditory region, abutting the petrosal bone and ventrally the bulla itself if the latter is present. Within this margin, the basioccipital is grooved or channeled for the inferior petrosal venous sinus. If this channel is on the lateral surface and is faced by a corresponding sulcus in the petrosal, a canal is thereby formed, termed here the petrobasilar canal. Posteriorly along this margin, the basioccipital may be emarginated and contribute to the occipital edge of the posterior lacerate foramen. On the ventral surface of the basioccipital are scars or rugosities upon which insert the longus capitus and the rectus capitis ventralis muscles, which act to pull the head ventrally.

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The exoccipital bones carry posteriorly the occipital condyles and anteriorly form the posterior margin of the auditory region. They are typically produced into paroccipital processes, upon which insert a variety of neck muscles. These processes may be closely appressed to the back of the bulla (as in feloids) or elongated into a distinct process directed ventrally or posteriorly. A hypoglossal foramen or canal pierces the exoccipital, providing passage for the exit of the hypoglossal nerve (XII), and perhaps a vein in some forms (see Guth, 1964). On the internal surface of the excccipital, a canal extends from the sigmoid sulcus posteriorly to open on the internal surface of foramen magnum; in life, this canal carries the occipital vein from the sigmoid sinus to the vertebral sinus.

In the adults of many mammals, the basicccipital fuses with the exoccipital, and the latter with the supraoccipital, to form what is generally knowm as the occipital bone. The position of the sutures between the separate elements listed above are not generally visible in the adult. Two other "fusion bones" represent the co-ossification of multiple, distinct elements in some forms: the "temporal bone" (terminology from human anatomy) and the sphenoid bone (Starck, 1967: 480). Since much of the nomenclature is based on that developed for human anatomy, many texts will discuss the occipital, or

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the temporal, even of animals in which the degree of fusion between the component elements is not nearly as extensive as in Homo. There are two disadvantages to this practice: first, the language becomes unnecessarily cumbersome, with the only benefit (and a very dubious one at that) being that it implies the human condition for comparison. Compare "pars squamosa of the temporalis" with "squamosal", for example.

The other detriment is that such terminology implies incorrect homologies, and makes it very confusing to sort out dermal, endochondral, and membrane bones. For example, the petrosal is largely an ossification of the otic capsule and therefore endochondral (with some membrane bone extensions), and a feature characteristic of at least gnathostomes. (Of course, the pars cochlearis of the petrosal is found only in mammals, and in a different form in birds, in which the cochlea is straight.) The squamosal and ectotympanic are dermal in origin, and are both elements thought to have been present in the common rhipidistian ancestor if not in the osteichthyan ancestor, in some form. Entotympanics, however, are usually membrane bone, in Patterson's (1977a) sense of the term; most are preformed in cartilage and are generally believed to be neomorphs in eutherians. Yet all of these--petrosal, squamosal, ectotympanic, and entotympanics--are frequently all considered part of one

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bone, the temporal, because all these parts are extensively co-ossified in adult humans. A failure to realize that the human terminology is an oversimplification can lead to rather great errors in discussions of other groups: "squamosal" is frequently taken at a superficial level to be a general synonym of "temporal", for example, which apparently led Eisenberg (1981: 120) to make the surprising statements that arctoid and cynoid carnivorans have bullae "composed almost entirely of the squamosal bone", and that the feloids have bullae "composed of a portion of the squamosal bone and an expanded portion of the endotympanic bone". This is a clear example of the sort of misinformation that ambiguous terminology can generate.

Since the goal of any comparative study is to understand more than one species, we are best served by terminology that is most widely applicable. Therefore I reject the convention that terminology from human anatomy is the standard (*contra* Cartmill, 1975, for example), and will use separate names for the elements consistently distinct in at least some mammals. Fusions can then be easily described in terms of those elements.

Figure 24 illustrates the main elements in the basicranium of an ossifying dog skull. Anterolateral to the occipital elements, ossification of the otic capsule produces the petrosal bone. As MacIntyre (1972) pointed

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out, the petrosal may best be visualized roughly as an elongate tetrahedron, or more precisely, as a three-faced ovoid anteriorly (the petrous portion) and a roughly pyramidal portion posterolaterally (the mastoid portion). On the petrous portion there are distinct faces, one facing the squamosal bone anterolaterally, a second facing dorsomedially (the cerebellar side), and a third facing ventrally (the tympanic surface). The mastoid portion projects dorsally, forming the posterolateral corner of the braincase, and laterally is produced in many taxa into a mastoid process for muscle attachments. This latter process may become ventrally elongate in response to modifications of the jaw musculature.

As already mentioned above, the medial margin of the petrosal carries a sulcus for the inferior petrosal sinus, and thus forms the lateral wall of the petrobasilar canal if one is present. In the posteromedial corner of the petrosal, an emargination marks the position of the posterior lacerate foramen. Within this emargination (sometimes termed the jugular notch) lies the aperture of the cochlear aqueduct, the bony canal into the cochlea providing passage for the perilymphatic duct. The ventral face of the petrosal is produced into a promontorium, and bears the fenestra vestibuli (across which the footplate of the stapes fits) and the aperture of the cochlear fossula (within which is the cochlear fenestra closed by

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the secondary tympanic membrane). In taxa with the internal carotid artery and nerve coursing in a lateral position across the promontorium, the surface of the latter may bear grooves or even enclosed tubes for these structures.

At the dorsal-most edge of the squamosal face of the petrous portion, a sulcus is present in taxa possessing a superior petrosal venous sinus of significant size. The crista petrosa, running along the dorsal margin down to the anteromedial apex, constitutes the edge between the squamosal and cerebellar faces. Variably placed somewhere on the anterior margin of the petrosal, the hiatus facialis is the aperture of the passage of the greater superficial petrosal nerve through the petrosal from its origin as a branch of the facial nerve (VII) at the geniculate ganglion. The nerve passes out of the hiatus facialis, and between the sphenoid and the petrosal, either through a persistent piriform fenestra or through a foramen left in the suture between these elements. It then travels diagonally on the ventral surface of the basisphenoid to the posterior aperture of the pterygoid canal.

On the cerebellar face of the petrosal, the largest feature is the internal auditory meatus, the aperture through which the facial (VII) and auditory (VIII) nerves, in company with various blood vessels, enter the otic

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capsule (see Figure 25). Dorsal to the internal auditory meatus, the subarcuate fossa may be more or less distinct; there is both taxonomic and ontogenetic variation in this structure (Miller et al., 1964: 19). The posterior margin of the intracranial surface of the petrous portion of the petrosal is delimited by the sigmoid sulcus descending from the transverse sulcus above down to the posterior lacerate foramen. In the petrous margin of this sulcus, the vestibular aqueduct opens into a slitlike fossa: the aqueduct is the bony passage through the petrosal for the endolymphatic duct, and the slitlike fossa houses the endolymphatic sac, which protrudes out between two layers of the dura mater (Bast and Anson, 1949). Some taxa have a foramen in the posterior wall of the sigmoid sulcus, through the wall of the mastoid to the posterior surface of the skull. Guth (1964) showed this for the dog and found that a vein passed through it from the sigmoid sinus.

Several bones in the auditory region may have membrane bone outgrowths helping to roof the tympanic cavity--i.e., epitympanic wings. In mammals the petrosal most constantly has at least a posterolateral wing developed, which develops from the crista parotica of the ventral face of the petrosal. This is the tegmen tympani, which grows anteriorly to roof over a large portion of the tympanic cavity. At the base of the mastoid process, the

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crista parotica forms the hyoid process, to which is attached the tympanohyal of the hyoid apparatus. In some forms, such as Homo, proximal segments of the hyoid apparatus are actually fused to the petrosal, and form an elongate process from the auditory region. In humans, both tympanohyal and stylohyal are fused, so that the resulting process is termed the styloid process. De Beer (1937) apparently considered the hyoid process in the domestic cat to be a styloid process proper, but this is contradicted by the presence of identifiable tympanohyal and stylohyal elements within the hyoid chain. Thus identification of the point of attachment of the hyoid apparatus as a styloid process is not sufficient assurance that such a process represents more than merely the point of articulation of the hyoid on the crista parotica, because of the tendency to use nomenclature from human anatomy even when the latter has incorrect implications for the homology of the structure in question. Consequently, I have used the neutral "hyoid process" unless more specific (usually ontogenetic) information is available.

The tegmen tympani is excavated for various structures of the middle ear. At its lateral edge, above and medial to the tympanic membrane, a distinct fossa, the epitympanic recess, houses the incus, head of the malleus, and the articulation between the two ossicles. A

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secondary recess may be present within the epitympanic recess proper for the short arm of the incus, which is moveably connected to the roof of the tympanic cavity by ligaments. Anteromedial to the epitympanic recess, a large fossa, the fossa muscularis major, is the site of origin of the tensor tympani muscle. In some carnivorans, this fossa is almost completely floored over by a thin sheet of bone, so that the origin of the muscle is deep in a bony pocket. Posterior to the fossa muscularis major, right at the base of the promontorium, the facial sulcus is present as a groove or enclosed tube in the tegmen tympani, from the facial foramen anteriorly, extending laterally dorsal to the fenestra vestibuli, posteriorly to the medial wall of the mastoid process, and then ventrally to the exit of the facial nerve from the tympanic cavity via the stylomastoid foramen. This sulcus is typically present as a very distinct groove or channel in the median face of the mastoid process; the stylomastoid foramen itself is formed by the bullar elements, which may also extend dorsally to form a median wall to the channel in the mastoid process. Near the point where the facial sulcus dives ventrally along the mastoid process, the stapedius muscle originates in a fossa muscularis minor. Developmentally, there may be present a distinct anterior epitympanic wing of the petrosal as well as the more lateral tegmen tympani, but these are indistinguishably

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fused in the adult in almost all cases (MacPhee, 1981), and no attempt will be made to distinguish between them here.

The squamosal bone forms part of the side of the brain case above the auditory region, the posterior part of the zygomatic arch, and the bony fossa for the articulation of the mandible with the skull. Above the external auditory meatus, the squamosal is frequently formed into a sharp edge or even a shelf, forming the roof to the meatus. A postglenoid foramen is primitively present, providing egress for the superior petrosal sinus (part of the external jugular drainage). It may be found in a variety of positions within the squamosal portion of the auditory region, anywhere medially or laterally within the posterior wall of the pedestal above the glenoid fossa, to more posteriorly within the shelf overhanging the external auditory meatus.

A variable amount of the mastoid process may be derived from a portion of the squamosal co-ossified with the mastoid portion of the petrosal; van der Klaauw (1931: 138) followed van Kampen (1905: 353) in distinguishing the squamosal contribution to this process from the mastoid and terming the former a posttympanic process. Because the suture is not always visible, and the process is functionally one process, I have not tried to distinguish between posttympanic processes and mastoid processes

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proper. The degree of squamosal contribution may be a useful taxonomic character, but will require ontogenetic information in many cases to determine the condition of the character in each taxon.

In mammals in general, the constant element in the floor of the tympanic cavity is the ectotympanic (or "tympanic ring"), the bone supporting the tympanic membrane. Primitively, and also initially in development, the ectotympanic is horseshoe-shaped rather than ringlike; the anterior horn attaches to the squamosal behind the postglenoid process, often in a pit, and the posterior crus to the anterior or anteromedial face of the mastoid process. In a variety of taxa, in which the two arms may or may not meet dorsally to form a closed ring, the ectotympanic is expanded either medially, so that it floors more of the tympanic cavity, or laterally, producing an osseous external auditory meatal tube, or both; any of these possible expansions also results in an ectotympanic that is not ringlike. Because of either of the possiblities, therefore, the term "tympanic ring" should be avoided in favor of the term "ectotympanic".

On the internal surface of the ectotympanic, the pars tensa of the tympanic membrane is attached to a sulcus in the bone via ligaments. The medial margin of this sulcus is produced into a sharp ridge, the crista tympanica. This sulcus and ridge extend around most of the diameter

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of the opening except dorsally, where the pars flaccida of the tympanic membrane is present, dorsal to the malleus.

The tubal cartilage covers the auditory tube along most of its length between pharynx and tympanic cavity, and therefore passes through an aperture in the anteromedial corner or anterior wall of the osseous bulla. In some forms, the lips of this osseous tubal aperture are elongate, forming a short tube, while in others, partial septa partition off a bony channel for the tubal cartilage. According to MacPhee (1981: 15) the tubal cartilage is a mammalian neomorph not clearly derivable from the visceral skeleton. MacPhee (1979: 36; 1981: 26) also stated that the rostral entotympanic in some taxa apparently develops in continuity ab initio with the rear portion of the tubal cartilage. This appears to be the case in Procavia, Dasypus, and Tupaia. In contrast, the primordium of the rostral entotympanic is seen to arise independently from, although it may later fuse with, the tubal cartilage in Myotis, Rousettus, Cynocephalus, and macroscelideans. There is apparently not yet any published information on this point for carnivorans.

Another important feature of the anterior margin of the bulla is the Glaserian fissure. During ontogeny, Meckel's cartilage passes through the fissure between the squamosal or alisphenoid bones bordering the auditory region anteriorly and the ectotympanic, and second,

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between the ectotympanic (and other flooring elements) and the tympanic roof. Later, Meckel's cartilage becomes discontinuous, but the blood vessels and nerves that passed through the fissure in association with the cartilage persist--most notably the chorda tympani nerve (which ran along the inner aspect of Meckel's cartilage) and the inferior ramus of the stapedial artery if the latter is present. This fissure is termed the "petrotympanic fissure" in human anatomy, but I follow MacPhee (1981: 55) in preferring the eponymous name "Glaserian fissure" because the former term is not descriptive of the condition in most animals.

The ectotympanic forms a variable amount of the floor of the tympanic cavity. In some taxa, such as ursids, otariids, and lutrine and mephitine mustelids among the Carnivora, and members of the Insectivora, Artiodactyla, Perissodactyla, Cetacea, Rodentia, Lagomorpha, and Proboscidea, the bulla is composed largely or entirely of the ectotympanic element (Novacek, 1977). It may be quite inflated relative to the size of the skull, as in many rodents, and in adults is frequently quite difficult to establish as a true (ecto)tympanic bulla rather than a composite bulla.

In many mammals, other elements contribute to the composition of the auditory bulla. Novacek (1977) listed the following additional major elements, in addition to

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the ectotympanic, as producing a tympanic process or otherwise contributing to the floor of the bulla: 1) entotympanic, 2) petrosal, 3) basisphenoid, 4) alisphenoid, 5) basioccipital, 6) exoccipital, 7) squamosal and 8) pterygoid. Within the Carnivora, however, of these possibilities, only an entotympanic contribution has been demonstrated. In all taxa examined by Hunt (1974a) in his review of carnivoran bullae, he found a rostral entotympanic associated with the internal carotid artery, and at least one separately ossifying caudal entotympanic.

On the basis of the relative contribution from ecto-and entotympanics and the internal structure, Hunt recognized five types of bullae within the order. The taxa with largely ectotympanic bullae were listed above and exemplify his Type A bulla. The remaining Carnivora had larger contributions from one or more entotympanics. Hunt's Type B bulla, which may be inflated or not, has a larger caudal entotympanic. This type is seen in Procyonidae, Canidae, musteline, guline, meline, and taxidiine Mustelidae, and Phocidae. The ventral and posterior regions especially of the bulla are often supported by struts and partial septa (from the caudal entotympanic), although in the arctoids these are variable and not considered homologous at any level with either the more constant, partial (entotympanic) septum in canids or

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the complete, bilaminar or ectotympanic septa in feloids. Invasion of the mastoid by the tympanic cavity frequently accompanies this type of bulla.

The bullar structure of the African palm civet (Nandinia binotata) constitutes Hunt's Type C--a shieldlike ectotympanic with a curled medial edge forming a low septum, but displaying incomplete to nc ossification of the caudal entotympanic, so that the main part of the bulla remains cartilaginous throughout life. Although Hunt (1974a) said that a septum is entirely lacking, and Clark and Guensburg (1972) consider Hough's (1953: 97) description of this curled medial edge to be erroneous, I observe a low inturning of that edge, which might be the remnants of an ectotympanic contribution to a septum; I do emphatically agree that Hough was totally incorrect in her assertions that the upturned margin of such a demi-bulla touched the promontorium, however.

Although a cartilaginous bulla has been considered by some authors to be the primitive condition for many eutherian groups and to have been present in many now extinct taxa (e.g. van der Klaauw, 1931), it is far more likely that the original tympanic capsule was floored by a fibrous membrane, like that apparently occurring in all mammals during ontogeny (MacPhee, 1981: 14). Cartilaginous bulla are rare, and occur in isolated taxa within otherwise well defined groups, and are therefore

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likely to be a neotenous retention (i.e. autapomorphous) in those taxa. (see the discussion in Novacek, 1977: not all of his supporting arguments are valid, but many are and I therefore agree with his conclusions.) The condition in Nandinia is therefore considered here a very specialized one (including perhaps secondary reduction of a septum) rather than necessarily a primitive one. In Nandinia, a small rostral entotympanic is present, associated with the internal carotid artery and close to the internal carotid foramen. As in many viverrids, the petrosal protrudes ventrally on the medial side of the auditory region so that it is visible externally between the entotympanic and the basioccipital.

In the Felidae, the Herpestidae, and the remaining Viverridae (Type D bulla), there is a septum dividing the bullar cavity nearly completely. This septum is bilaminar, developing from both the ectotympanic and the caudal entotympanic. Hunt (1974a: 42) restricted the term "septum bullae" to only a bilaminar septum like that described by Wincza (1896: 330) for the domestic cat, so that his Type D bullae are the only divided bullae with a true septum bullae under his definition. The anterolateral chamber resulting from this division is thus floored by both ectotympanic and rostral entotympanic, and the posterior chamber by caudal entotympanic. Although the bulla itself is rather inflated in these forms, there

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is no invasion of the surrounding basicranial bones by the tympanic cavity.

The final type of carnivoran bulla is also double chambered. In the hyaenid bulla, a full septum is again present, but the nature of that septum is less clear. It is generally thought to be unilaminar and ectotympanic, based on Hunt (1974a) and therefore very different from the septum bullae proper of felids and viverrids (but see further discussion in the character analysis, p. 388). In both hyenas and the aardwolf, the ectotympanic chamber is greatly inflated, so much so in hyenas that initial description of the hyena tympanic region characterized it as being single chambered (Flower, 1869). Pocock (1916b) subsequently found the "posterior" chamber, in this case entirely dorsal to the hypertrophied ectotympanic chamber, and even partially expanded into the adjacent mastoid bone.

In carnivorans, the medial wall of the bulla frequently reflects in its bony structure the path of the internal carotid artery in some fashion. Hunt (1974a) demonstrated a separate, rostral entotympanic in felids, viverrids, and canids among the Carnivora, and deduced its presence by identification of sutures in the bullae of the remaining families. He found in all cases that the internal carotid artery lay along the ventral edge of the rostral entotympanic, and when enclosed in a carotid

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canal, was so enclosed only in proximity to the rostral entotympanic, which contributed to the canal. In most carnivorans, a deep sulcus or more often a completely enclosed canal is present. The major exceptions are in those taxa in which the internal carotid artery is greatly reduced (e.g. felids) and variably within some other groups (e.g. some viverids).

A problem of homology (and nomenclature) exists for the foramen or foramina by which various blood vessels enter the skull at the anteromedial margin of the bulla. A "promontory foramen", lateral to and separated from a "median lacerate" or "carotid foramen", has often been identified for the entrance of the "promontory artery" into the cranial cavity (e.g. Hunt, 1974a: 32). This will be discussed fully in the context of more recent evidence about carotid artery homologies in the later section on character analysis (p. 408). Some introductory points need to be made in this introduction to the anatomy of the region, however, primarily to explain my terminology.

First, note that no living mammal has ever been demonstrated by direct observation to have simultaneously both a promontory artery and a medial carotid artery, and therefore the simultaneous presence of both foramina has not been demonstrated either. Certainly a more lateral foramen is to be expected in that region, but for passage of the pterygoid nerve towards the pterygoid canal rather

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than for another blood vessel entering the braincase. If in fact the promontory and medial carotid arteries are homologous vessels but in different positions in different taxa (Presley 1979), then only one foramen for the internal carotid artery will ever be present.

The question then remains of an appropriate name for this foramen, since many have been applied. Perhaps the most widely used is "median lacerate foramen"; the corresponding aperture in the human skull is termed the foramen lacerum (medium). However, so much confusion surrounds the term "median lacerate foramen" that I have concluded that it is best to avoid it altogether. Less ambiguous terms are available for all the structures to which reference is necessary in the discussion presented here. Justification for the terminology chosen requires, however, a broader consideration of the names of several apertures, and of some features in the development of the mammalian skull.

Three "lacerate foramina" have been named on the mammalian skull; all are remnants of fissures between developing cranial bones, providing passage for nerves or blood vessels or both. The most anterior, the "anterior lacerate foramen", is the persistent opening in the suture between the orbitosphenoid bone and the alisphenoid bone. During development of the eutherian chondrocranium, this foramen is bounded posteriorly by the ala temporalis, and

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anteriorly by the orbital cartilage and its connection to the posterior part of the trabecular cartilage, the pila metoptica. Dorsally, the orbital cartilage grows posteriorly, completing the enclosure of the foramen with the taenia marginalis. This opening provides passage for several nerves, an artery, and a vein between the anterior portion of the cranial cavity and the orbital fossa. The anterior lacerate foramen is now more commonly called the sphenorbital foramen, the orbital fissure, or similar term (see Glossary entry under sphenorbital foramen).

Posterior to the ala temporalis "is the middle lacerate foramen which lies close to the entrance of the internal carotid artery into the cranial cavity" (Moore, 1981: 41). The fissure between the ala temporalis and the otic capsule is not typically confluent with the internal carotid foramen, however. In reptiles, monotremes, and metatherians, the carotid foramina in the chondrocranium are enclosed within one or paired foramina bounded by the trabeculae anteriorly, the polar cartilages laterally, and the parachordals (basal plate) posteriorly, well medial to the otic capsules. During ossification of the cranial floor, the internal carotid foramina become completely surrounded by the basisphenoid, resulting in the rather anterior and medial position of the foramina characteristic of reptiles and noneutherian mammals.

In eutherians, the polar cartilages appear to have

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moved medially to the entrance of the internal carotid artery, but the foramen on each side for the internal carotid artery is still bounded laterally in the chondrocranium, now by a structure new to eutherians, the alicochlear commissure. The latter connects the anterior margin of the otic capsule with the ala temporalis, separating the internal carotid foramen medially from the gap between the ala temporalis and otic capsules laterally. After ossification of the cranial floor, the internal carotid foramina are usually more posteriorly placed relative to the auditory region, and frequently hidden by more superficial structures in that region. The basisphenoid now partly marginates the internal carotid foramen, rather than completely enclosing it.

"Piriform fenestra" has been applied to a persistent gap between the alisphenoid and the petrosal (McDowell, 1958; 128). Its meaning was subsequently broadened by MacPhee (1981: 59) to the "large gap, seen in all fetal and a few adult mammals, that lies between the auditory capsule and its dorsal outgrowths (tegmen tympani, epitympanic wing of petrosal) on the one hand and the epitympanic wings of the sphenoid and squamosal on the other." The piriform fenestra is bounded medially, and separated from the internal carotid foramen, by the alicochlear commissure; it transmits the greater and deep petrosal nerves towards the pterygoid canal.

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The confusion about the meaning of the term "median lacerate foramen" becomes apparent when one considers, in the light of the above relationships and terms, the following meanings which have been given to this one term:

1) in humans, the aperture through which the internal carotid artery enters the skull (e.g., Cunningham and Romanes, 1972: 117),
2) a cartilage-filled foramen that transmits only small structures in Homo--the pterygoid nerve and small accessory meningeal branch of the ascending pharyngeal artery (Cartmill, 1975: 317-318),
3) in forms with more complete ossifications, the foramen for this latter artery only (Cartmill, 1975: 318),
4) the lateral portion of the petrotympanic fissure, cut off from the internal carotid foramen, i.e. the piriform fenestra (e.g. Pocock, 1916a: 268 and Van der Klaauw, 1931: 114), and
5) very different foramina altogether (e.g., a foramen transmitting the inferior ramus of the stapedial artery, Greene, 1935: 16; see below).

Two examples will complete the picture. First, van der Klaauw (1931: 113ff) used medial and anterior lacerate foramen interchangeably, as if they were synonymous. Further, Jollie (1962) labeled a gap at the anteromedial corner of the petrosal as the "anterior lacerate

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fenestra", as did Flower (1869). The second example is slightly more complicated. Greene (1935: 16) identified a foramen entirely enclosed within the sphenoid as a "middle lacerated foramen for pterygopalatine branch of internal carotid artery." As she suggested, the pterygopalatine branch appears to correspond to the stapedial artery of other authors. The exit of this vessel from the anterior margin of the tympanic region (through the Glaserian fissure, or in this case, a true petrotympanic fissure) is, in Greene's illustrations (e.g. Figure 210, p. 248), immediately adjacent to the path of the chorda tympani; the vessel thus corresponds to the inferior ramus of the stapedial artery of other authors (e.g. Bugge, 1974). In most mammals, the inferior ramus, if present, joins the internal maxillary artery anterior to the auditory region and passes through the alisphenoid canal. In Figure 209 (Greene, 1935: 248), the main trunk of this pterygopalatine artery does indeed go next through the alisphenoid canal.

Greene's Figure 209 shows the vessel entering the "middle lacerated foramen" to be a medial branch from the main trunk of the stapedial, or at least from the inferior ramus; this branch is labeled the "pterygoid portion of pterygopalatine", "artery of the pterygoid canal", or "Vidian artery". If the identifications of the vessels are correct, then the foramen in question is the posterior

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opening of the pterygoid canal, a channel between the pterygoid and basisphenoid bones, and not a middle lacerate foramen. However, my examination of a cleared and alizarin-red stained skull of a 22-day fetal rat (Rattus norvegicus) in the University of Connecticut teaching collection supported the conclusion I drew from an adult skull, that the foramen is not bounded by pterygoid, but instead by either basisphenoid alone or basisphenoid medially and alisphenoid laterally.

Unfortunately, it is not possible to determine the answer to this problem from Bugge's (1974) review--further dissections of the intracranial course of these vessels would be required--but I suggest that perhaps Greene's "middle lacerate foramen" is actually a quite medially placed foramen ovale, and that the artery she observed entering this foramen is an anastomosis from the ramus inferior plus the external carotid to the middle meningeal artery.

Regardless of the accuracy of my hypothesis, the labelling of this foramen as a middle lacerate foramen is a good example of the rather arbitrary and inconsistent fashion in which this term has been used in the past. In this case, the presence more posteriorly of an internal carotid foramen is clearly indicated: the end of a bristle inserted into the carotid canal appears intracranially at the anteromedial apex of the petrosal,

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next to the sella turcica, which is exactly the position of the internal carotid foramen in the vast majority if not all eutherians. In ventral view, the internal carotid foramen in Rattus is thus hidden from view by the anteromedial corner of the osseous auditory bulla. Finally, one may note that Rattus displays a large open fissure between the anterior and lateral margins of the petrosal/tympanic complex and the adjacent alisphenoid and squamosal bones; at least the anterior arm of this fissure, which is what one might have expected to be labelled a median lacerate foramen, can surely be appropriately termed a persistent piriform fenestra.

In summary, the contradictory uses of the term "median lacerate foramen" have rendered it largely useless, especially in light of the more consistent meanings attributed to "piriform fenestra". I agree with MacPhee (1981: 41) that a distinction between a "promontory foramen" and "medial carotid foramen" is inaccurate, and with Cartmill (1975: 317) that "anterior carotid foramen" is misleading because of the use of "anterior carotid artery" by some authors for the anastomosis between the ascending pharyngeal and the internal carotid arteries. In light of the lack of a clear consensus on a preferred term here as well, I will use "internal carotid foramen" as defined in the glossary, following Miller et al. (1964). This term has the benefit

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of close correspondence with a largely undisputed arterial name; the modifier "internal" may also be accurately taken as reference to this being the passage through the floor of the cranial cavity proper, no matter what foramina have been formed by the ends of bony canals through more superficial basicranial elements (e.g. the carotid canal through the entotympanic in carnivorans).

Cartmill (1975: 317) cited a need for names for both ends of the carotid canal. "Posterior carotid foramen" for the posterior end is already well embedded in the literature, and is so used here. "Anterior carotid foramen" would be a logical choice for the anterior end of the same canal (and has been so used by Hunt, 1974a), but has the drawback of having been used in a variety of other ways previously, and still having some implication of reference specifically to the anterior carotid artery of Saban (1963: e.g. 176; discussed further in Cartmill, 1975). I have not found a need in my descriptions for a term for the anterior opening of this canal, and have therefore not settled on one here.

Problems also exist with the nomenclature for the third such persistent foramen, in the gap between the occipital arch and the auditory capsule, constituting the posterior lacerate foramen. This term has been widely replaced by "jugular foramen"--a counter-productive move because of the implications of the latter name. In most

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eutherians, the sigmoid venous sinus, the inferior petrosal venous sinus, and the ninth, tenth, and eleventh nerves all share the same egress from the skull, through a gap that is a remnant of the metotic fissure. Usually, the two venous sinuses join in the vicinity of the foramen to form a vessel generally termed the internal jugular vein (although some authors call the confluence there the inferior cerebral vein and identify the jugular further down the neck after the entrance of the lingual vein, the occipital vein, and several veins from the pharyngeal area). In some taxa, however, not only do these sinuses join well outside this foramen (not an usual condition, apparently), but a bony partition is present between the apertures from which the two sinuses exit. Since the nerves are evident earlier in ontogeny than are the blood vessels, I consider the name of the foramen to go with the aperture for the nerves, and propose that a separate exit for any venous sinus be named after that sinus or passage. In the Carnivora, the petrobasilar canal sometimes has a separate aperture--hence the petrobasilar foramen (see Glossary). This morphological variation renders the name "jugular foramen" potentially misleading; the original term, "posterior lacerate foramen" is therefore preferable for the remnant of the metotic fissure.

Those elements bordering the auditory region anteriorly have been mentioned, but may be summarized now.

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The "sphenoid" is the third major fusion bone (Starck, 1967) in the primate skull. In many other taxa, separate elements can be recognized, of which the basisphenoid (a median element) and the alisphencid (paired) concern us here. As described above, the endochondral basisphenoid still forms part of the margin of the internal carotid foramen in eutherians. It will also commonly have channels on its ventral surface for the tubal cartilage and the pterygoid nerve (leading to the pterygoid canal).

The alisphenoid is a membrane bone (sensu Patterson, 1977a) that provides passage for several nerves and blood vessels, thus containing within it the foramen ovale, foramen rotundum, and the alisphenoid canal if present. Either the alisphenoid or the adjacent portion of the squamosal may be grooved or channeled for the chorda tympani nerve and accompanying blood vessels leaving the tympanic cavity via the Glaserian fissure. Both or either the alisphenoid and basisphenoid may develop epitympanic wings posteriorly; because the lateral extant of the basisphenoid is difficult to determine in most adult carnivorans, I have not attempted to distinguish between the two, but have referred simply to "the epitympanic wing of the sphenoid" in most cases.

This topographic review of the ear region, although a necessary beginning, has failed to give a very good functional or developmental introduction to the region.

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Therefore, let us consider briefly the general plan of the auditory region in functional units, including the contents of both the middle and inner ears. Although only limited deductions about the soft anatomy can be made for fossil taxa, some understanding of the soft anatomy of the extant relatives helps the paleontologist stay oriented and perhaps distinguish more accurately between reasonable and unreasonable deductions about even the bony structure, much less inferences about circulation or other soft anatomy.

The eutherian ear may be divided into three functional components. First, the external ear is primarily a sound-gathering device, and comprises the auricle or pinna (the visible part of the ear) and the cartilaginous and bony external auditory meatal tube, leading into the middle ear. The second segment is that middle ear, bounded laterally and externally by the tympanic membrane stretched inside the osseous external auditory meatus, bounded dorsally, medially and ventrally by the tympanic roof and bulla, and bounded internally by the footplate of the stapes across the fenestra vestibuli.

Contained within this middle ear is the tympanic cavity, an air-filled space (even in aquatic mammals; Fleischer, 1978: 7) surrounding the chain of three auditory ossicles and their associated ligaments and two muscles. An aperture at the anterodorsal corner of the

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tympanic cavity is the opening of the auditory tube, which connects this cavity with the pharynx. Various subdivisions of the tympanic cavity are frequently recognized, especially distinctions among the spaces contained within the epitympanic recess dorsally, the tympanic cavity proper (the rest of the space immediately surrounding the ear ossicles), and the hypotympanic sinus, or ventral or fundic portion of the cavity. Distinguishing among these subdivisions is difficult, and was not found to be particularly useful. It was noted in the descriptions, however, when the bulla was particularly inflated or when the tympanic cavity was enlarged by an excavation or formation of sinuses in the cranial bones surrounding the auditory region.

The middle ear functions to conduct the vibrations from the relatively large area of the tympanic membrane via the malleus, incus, and stapes, to the much smaller area of the footplate of the stapes in the fenestra vestibuli, thus increasing many fold the amplitude of the sound waves (22 times in the domestic cat, according to Crouch, 1969: 325). Many aspects of middle ear function have been well summarized by Fleischer in his 1978 monograph. He pointed out, for example, that the increase in pressure at the stapedial end of the chain is also due in small part to leverage resulting from the relative lengths and angles of the various arms and processes of

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the three ossicles. The relative size of the pars flaccida of the tympanic membrane affects the effective volume of the contained air space in the tympanic cavity. Both middle ear muscles afford some control of the vibration of the ossicular chain, perhaps dampening the response of the chain to continued loud noise.

As Fleischer (1978: 9) noted, the basic membrane-bounded ear cavity is subject in low frequency reception to disturbances in sensitivity as a result of deformation of the tympanic cavity caused by motions within the head, such as swallowing. The mechanical solution to this is the development of a bony wall--the osseous auditory bulla. Another difficulty was posed by the increase in size within the Mammalia and the increase in neural complexity: a main blood supply to these regions was through the stapedial artery, which passed through the foramen in the stapes. Since middle ear structures do not increase in size proportionally to the weight of the animal, blood supply to these regions had to be rerouted. In any case, one cannot help but think that a decrease in auditory acuity must have been caused by a major artery roaring and pulsing through the stapes.

Once to the footplate of the stapes, the vibrations have passed through the middle ear and are entering the third segment, the inner ear. In mammals, this structure comprises organs sensing sound (the cochlear portion),

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movement (the semicircular canals), and direction of gravity or other acceleration (the utriculus and sacculus). These organs constitute a membranous, fluid-filled (endolymph) labyrinth, floating in fluid (perilymph) within a bony labyrinth inside the petosal.

The homologies of the structures in the middle and inner ear are indicated fairly clearly by their embryology. Although not evident by their close structural relationship in the adult, the middle and inner ears develop from very different sources (Gardner et al., 1960: 687; Cunningham and Romanes, 1972: 831). An ectodermal thickening, the auditory placode, invaginates, separates from the surface, and sinks into the mesoderm to form the otic vesicle beside the hindbrain at the level of the seventh and eighth cranial nerves. A dorsal diverticulum becomes the endolymphatic duct, or vestibular aqueduct, leading to the endolymphatic sac inserted between meninges of the brain. From the posterodorsal portion of the vesicle, three disk-like evaginations appear, their centers coalesce, and the semicircular canals remain. The ventral part of the vesicle sends out an extension which, as it lengthens, coils to form the cochlea. As various constrictions and elongations continue to form the details of the labyrinth, the ectodermal epithelium differentiates into the various sensory structures of the different regions.

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As the differentiation of the ectodermal membranous labyrinth takes place, the mesodermal connective tissue in which the otic vesicle is embedded is also differentiating. The loose, reticular layer of tissue immediately around the labyrinth is gradually absorbed, leaving a space that is filled with perilymph. An outer zone of cartilage, the otic capsule, is eroded and remodeled as the membranous labyrinth develops, so that the shape of the ectodermal labyrinth is reflected in the structure first of the otic capsule and then of the ossified petrosal.

While this elaboration of the otic vesicle is occurring, dorsal wings from the first and second pharyngeal pouches coalesce and form an evagination--the tubotympanic recess. This pouch grows out to lie against the ventrolateral wall of the condensed mesenchyme around the otic vesicle, carrying with it cartilages of the first and second pharyngeal arches (shown in Figure 26). The ossifying otic capsule develops an epitympanic wing that grows forward and laterally over the tubotympanic recess--the tegmen tympani.

Between the tubotympanic recess and the tegmen tympani, the dorsal ends of the pharyngeal arch cartilages articulate with each other. The cartilage of the first arch, Meckel's cartilage, gives rise in its posterior end to at least the head and manubrium of the malleus

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(homologue therefore of the articular and retroarticular; the anterior process of the malleus, the goniale, is dermal, and homologous with the reptilian prearticular). From the second cartilage develops the stapes (perforated by the often transitory artery of the second arch, and homologous to the osteichthyan hyomandibular bone) and proximally the incus (probably the homologue of the quadrate). (This second cartilage is often termed "Reichert's cartilage" in the literature: the more distal portion of it gives rise to at least the tympanohyal of the hyoid arch, and frequently additional hyoid elements as well.) Above this site of articulation between the cartilages and their endochondral derivatives, the tegmen tympani develops a concavity to house the incus and the articular head of the malleus--the epitympanic recess.

During the differentiation of the ossicles from the cartilages on each side of the tubotympanic recess, the extreme end of the recess expands dorsolaterally around the developing ossicles, so that the endodermal wall of the pouch from the pharynx covers the ossicles as well as the walls of the tympanic cavity with the mucus lining of the middle ear. The ossicles actually stay outside the pouch, although the pouch grows completely around them, in the same way that the gut is actually outside the coelom in a vertebrate, for example. The proximal part of the tubotympanic recess remains constricted, forming the

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auditory tube, beneath which a supporting cartilage develops late in ontogeny, in close association with the rostral entotympanic if the latter is present.

External to the pouch enclosing the tympanic cavity, on the ventral surface, the ectotympanic develops above the fibrous membrane that has developed flooring the tympanic capsule. It develops intramembranously, and is generally considered homologous to the angular of the reptilian lower jaw. Entotympanics almost always develop as endochondral bones, cartilage-replacement bones, within the fibrous membrane itself (MacPhee, 1979, 1981). This is an interesting example of an apparently neomorphic element that is not a membrane bone, but endcchondral instead--a situation for which Patterson's (1977a: 79) definition of "membrane bone" to include neomorphic or heterotopic bones does not work particularly well.

In summary, then, the innermost part of the inner ear, the fluid-filled membranous labyrinth, is ectodermal in origin (as are the other sensory structures and the central nervous system itself in vertebrates). The cartilaginous, then bony, labyrinth surrounding the stato-acoustic organs, the otic capsule and its ossification, the petrosal, is mesodermal, as are the pharyngeal cartilages and their endochondral derivatives, the ear ossicles. The air-filled middle ear cavity is lined with endoderm from the pharynx, with which it

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retains its connection via the auditory (or Eustachian) tube. Ossifications of the tympanic floor develop in a variety of ways: the ectotympanic is a dermal bone, most entotympanics appear to develop endochondrally (but within the fibrous membrane, so perhaps this is equivalent to adventitious cartilage), and tympanic processes develop generally as membrane bone outgrowths adjacent to the intratympanic surface of the fibrous membrane (MacPhee, 1981: 16).

Muscles inserting on the rear of skull and basicranium

The following outline gives a summary of the cranial muscles inserting on the basicranium and posterior surface of the skull. Only two muscles are actually enclosed deep within the middle ear, the m. tensor tympani and m. stapedius. Two additional muscles insert very close to or in the auditory region, the tensor and levator veli palatini muscles. The rest all insert on the edges of the auditory region--on the mastoid and paroccipital proceses and ridge between the two, a couple on the ventral surface of the basicccipital, and many on the lambdoid crest and nuchal shield.

A quick glance at the height on the nuchal crest, the rugosity of the shield, and the size of particularly the mastoid process in nimravids leads one to the conclusion that heavy neck and jaw musculature accompanied the

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development of saber-like canines. The significance of this for interpretation of the auditory region is twofold: first, while no muscles in extant carnivorans are known to insert on the auditory bulla itself, except on the styliform process at the anteromedial corner, especially no major ones controlling head or jaws, it is clear that many muscles insert around this region, and may affect proportions of the region by involving changes in lever arms or size of insertions. Second, the shape and position of the bulla itself may change in response to these muscle-related changes in surrounding structures, such as hypertrophy of the mastoid process, and will therefore be due to functional reasons extrinsic to the area we are studying.

The following outline of the cranial muscles is arranged from superficial to deep, and dorsal to ventral. Most of the information is from Crouch (1969) and Wessells and Center (1975).

M. ABDUCTOR AURIS BREVIS

origin: lambdoidal crest

insertion: medial surface of concha of external ear

action: pulls concha caudad

M. CLEIDOTRAPEZIUS (= M. CLAVOTRAPEZIUS, M. CLEIDOCERVICIS)

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origin: lambdoidal crest to middorsal raphe over axis

insertion: clavicle, on raphe with cleidobrachialis

action: draws clavicle craniodorsal

M. LEVATOR SCAPULAE DORSALIS

origin: lambdoidal ridge under m. clavotrapezius

insertion: scapula

action: rotates and draws scapula craniad

M. RHOMBOIDEUS CAPITIS (= M. OCCIPITOSCAPULARIS)

origin: medial half of lambdoidal ridge

insertion: cranial angle of scapula

action: rotates and draws scapula craniad

M. STERNOMASTOIDEUS

origin: manubrium of sternum

insertion: lambdoidal ridge, mastoid region

action: unilateral: turns head;
bilateral: flexes neck and depresses snout

M. BIVENTER CERVICIS (= medial portion of M. SEMI-SPINALIS CAPITIS)

origin: slips from spinous, cranial articular, and transverse processes of cervical and first three thoracic vertebrae

insertion: medial third of lambdoidal crest

action: unilateral: flexes head laterally;

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bilateral: elevates head

M. COMPLEXUS (= lateral portion of M. SEMI-SPINALIS CAPITIS)

origin: slips from spinous, cranial articular, and transverse processes of cervical and first three thoracic vertebrae

insertion: medial third of lambdoidal crest, lateral to m. biventer cervicis

action: unilateral: flexes head laterally;
bilateral: elevates head

M. RECTUS CAPITIS POSTERIOR (MAJOR AND MEDIUS)

origin: spinous process of axis

insertion: supraoccipital bone, ventral to medial part of lambdoidal crest

action: elevates head, raises snout

M. RECTUS CAPITIS POSTERIOR MINOR

origin: dorsal arch of atlas

insertion: supraoccipital bone, ventral to insertion of m. rectus capitis posterior major and medius

action: raises snout

M. SPLENIUS (broad sheet of muscle covering dorsal and lateral surfaces of neck)

origin: middorsal cervical fascia and ligament

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insertion: lambdoidal ridge to mastoid (lateral portion may be fused with m. longissimus capitis)

action: unilateral: flexes head laterally;
bilateral: elevates head

M. LONGISSIMUS CAPITIS

origin: by four tendons on anterior articular processes of cervical vertebrae four through seven

insertion: strong tendon to mastoid process (often united with m. splenius)

action: flexes head laterally

M. DIGASTRICUS

origin: mastoid process, paroccipital process, and ridge between them

insertion: ventromedial margin of mandible

action: depresses mandible, opens mouth

M. STYLOGLOSSUS

origin: mastoid process and stylohyal

insertion: tongue

action: retracts tongue

M. CLEIDOMASTOIDEUS (deep to m. sternomastoideus)

origin: mastoid process

insertion: clavicle and raphe lateral to clavicle

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action: pulls head down or draws clavicle forward

M. JUGULOHYOIDEUS

origin: paroccipital process

insertion: stylohyal

action: draws hyoid caudad

M. LEVATOR SCAPULARIS VENTRALIS (= M. OMOTRANSVERSARIUS)

origin: ventral surface of basioccipital and transverse prccess cf axis

insertion: metacromion and infraspinous fossa

action: draws scapula craniad

M. LONGUS CAPITIS (lies on ventrolateral surface of cervical vertebrae)

origin: by five head on margins of transverse processes of second through sixth cervical vertebrae

insertion: basisphenoid and basioccipital bones, medial to tympanic bulla (unites at insertion with m. levator scapularis ventralis)

action: depresses snout, draws head ventrad

M. RECTUS CAPITIS VENTRALIS (dorsal to and deep to m. longus capitis)

origin: ventral arch of atlas

insertion: basioccipital bone caudal tc insertion of

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m. longus capitis

action: draws head ventrad by depressing atlanto-occipital joint

M. RECTUS CAPITIS LATERALIS

origin: ventral surface of transverse process of atlas

insertion: fossa lateral to occipital condyle and on base of paroccipital process

action: flexes head laterad

M. TENSOR VELI PALATINI

origin: ventral surface of sphenoid between foramen ovale and groove for auditory tube (Reighard et al., 1935: 230); cartilage of the auditory tube (Cunningham and Romanes, 1972: 293); processus tubarius on anterior horn of ectotympanic (van der Klaauw, 1931: 132)

insertion: in aponeurosis in velum palatinum (soft palate)

action: stretches the palate

M. LEVATOR VELI PALATINI

origin: surface of basisphenoid medial to groove for auditory tube, and styliform process of bulla tympani

insertion: into the velum palatinum

action: elevates caudal part of soft palate

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M. STAPEDIUS

origin: fossa in lateral surface of petrosal caudal to epitympanic recess and close to fenestra vestibuli

insertion: head of stapes

action: pulls in a direction parallel to plane of footplate, forcing one side of the footplate into the vestibulum, and pulls the other side away from the petrosal; the annular ligament is thus acting as a spring between the footplate and the fenestra vestibuli.

M. TENSOR TYMPANI

origin: fossa muscularis major in epitympanic wing of petrosal (dorsocranial to fenestra vestibuli), or wall of auditory tube, or both

insertion: on transverse part of malleus, close to the base of the manubrium

action: tenses tympanic membrane (protecting against protracted loud noise), and tightens articulations of ossicular chain (Fleischer, 1978: 45).

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Glossary

Much confusion has surrounded the use and meaning of many of the terms identifying basicranial features. Since the function of a term is to communicate something, to refer specifically to something, such confusion over meaning is both self-perpetuating and immediately defeating to the larger goals of anatomical description and phylogenetic analysis. Why the latter is also affected is clear when one remembers that homologies and definitions of character states (upon which specific hypotheses of phylogeny are inescapably based) are implied by the identifications of structures, and those identifications are communicated from one person to another, or even encoded just in the original worker's notes, by words and labels. To dismiss a question as being merely one of semantics is to miss the fundamental point that it is only through language that we communicate historical ideas, and it is through language that we encode the details of our hypotheses.

Two sometimes conflicting parameters of language must be simultaneously maximized in order to increase efficiency and accuracy of communication: one aspect is the stabiliity of meaning (a sort of <u>accuracy</u> of language), so that most people associate the same meaning with a term. The other aspect, equally important, is <u>precision</u> of meaning and connotation, so that meanings are

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increasingly specific and precise, rather than vague or ambiguous. (This is not to say the concept, idea, or object reffed to becomes more precise, only that a worthwhile goal in science is that the correspondence of a word to a concept becomes tighter, no matter how vague or ambiguous is the concept to which the word refers. Lewis Carroll would have known exactly what I mean.) These two considerations--precision and accuracy in language--will sometimes be in conflict, but one will be aided in balancing competing demands by remembering the primary goal of accurate and efficient communication.

One useful response on the part of individuals is to define how they are using the more difficult, ambiguous, obscure, or disputed terms. By reference to the author's definitions, readers will be better able to understand the reasoning presented even if the reader usually uses some terms differently. Another potential benefit is that underlying concepts may be clarified in the author's mind or the reader's mind or both, reducing confusion and probably increasing the stability of terms' meanings. Therefore I applaud the efforts of various authors to discuss meanings explicitly and to offer definitions (e.g., Bast and Anson, 1949: 120; Cartmill, 1975: 317; MacPhee, 1981: 41).

On the same philosophical grounds I consider counterproductive any arbitrary rules, e.g.: "These

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definitions are based on the nomenclatorial assumption that the human nomina anatomica take priority where homology is known; that, if an ankle bone in some animal is believed to be homologous with the human talus, it is an error to refer to it as the astragulus." (Cartmill, 1975: 317). As was argued in the general morphological introduction for cranial bone homologies, a human is in many respects a very poor "type" animal because of a variety of rather extreme specializations, not least of which is bipedality and the attendant shifts in orientation of many structures. Granted, the human is and will likely remain the animal whose anatomy is known in most detail; in those cases in which specific detail is known only for the human, then hominid terminology will obviously apply.

But two other situations occur: in one (of which Cartmill gave an example), the structures in general are homologous and the terms used are fully synonymous (i.e. no differences in connotation, except perhaps one term implying that the tarsal element is from a hominid and the other that it is from some non-hominid mammal, because of current usage). There is nc real reason to use one over the other. The only problem caused is that students in the field have two words to learn to use and recognize rather than one. And this requirement will remain no matter how well future authors conform to the Nomina

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Anatomica if those students are going to read previously published works with comprehension.

The remaining situation, however, is more of a problem. For those structures in which Homo is very specialized, many terms will be inaccurate or misleading in their implied relationships and homologies when applied to animals not specialized in the same fashion. (A good example was the use of "temporal" to include squamosal, petrosal, and tympanic, discussed above.) In these cases, it is most important to work out a general terminology completely applicable to the primitive condition; specialized conditions, including the hominid condition, will then be describable in those more widely applicable terms. The greatest benefit will be that implied homologies and polarities will more nearly match current hypotheses. But clearly, in such cases, clinging to the terminology created for the hominid condition is counterproductive.

This, then, is the philosophy underlying the decisions I have made about specific terms to use and what I mean by them. In the following glossary, I have given the definitions of some terms as they are used in this report, as well as synonymies, or at least terms that sometimes have been used for the same structure. The main centers of ossification have been summarized in the previous section; most bones are therefore not listed. I

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have avoided using a latinized term to mean one thing and its gloss to mean another, because this practice introduces unnecessary confusion: it becomes impossible to translate the latinized version directly, since the translation has another meaning! Enough modifiers are available that such distinctions are unnecessary. I have not supplied glosses for all synonyms since they will usually be readily recognized when encountered in the literature (and I am not advocating their use in future studies). Glosses or latinized versions are from the Nomina Anatomica (third edition), unless referenced otherwise.

ANTEROMEDIAL PROCESS

synonyms: processus anteromedialis. (sometimes mislabelled the "styliform process", e.g. Reighard et al., 1935: 56; Field and Taylcr, 1950; Crouch, 1969).

an anteriorly directed projection from the anteromedial corner of the bulla, lying on or in a groove in the basisphenoid bone, medial tc the aperture for the tubal cartilage. In rodents, the styliform process appears to be in the same position as the anteromedial process of carnivorans and other taxa, perhaps the basis of the confusion in felid anatomy. The two are distinguished in

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skeletal preparations (in which the insertion of the m. levator veli palatini cannot be determined directly) by the relative position of the auditory foramen: the styliform process is on the ventral margin of the auditory foramen, whereas the anteromedial process is medial to the auditory foramen and directly appressed to the basisphenoid. (Van der Klaauw, 1931: 117; MacPhee, 1981: 46).

ASCENDING PHARYNGEAL ARTERY

synonyms: a. pharyngea ascendens, anterior carotid artery (see Cartmill, 1975).

branch from the external carotid artery, ventral to the auditory bulla, usually a small vessel supplying pharyngeal muscles; however, in some forms, including many carnivorans, this vessel is large and anastomotic with the anterior portion of the extracranial internal carotid, thus contributing to or taking over the carotid arterial supply to the circle of Willis intracranially.

AUDITORY BULLA

synonyms: bulla auditiva, tympanic bulla

the skeletal floor to the tympanic cavity, either cartilaginous or osseous, and either flat or inflated. The term "tympanic bulla" is to be avoided, because it is unclear whether an auditory bulla in general is meant, or specifically one composed entirely of the "tympanic

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bone"--i.e. ectotympanic.

AUDITORY TUBE

synonyms: Eustachian tube, tuba auditiva, pharyngotympanic tube.

Channel connecting the tympanic cavity with the pharynx; derivative from the gill pouch between the first (mandibular) and second (hyoid) pharyngeal arches, and considered homologous with the primitive gnathostome spiracular canal; supported by a cartilage (the "tubal cartilage"), with which the rostral entotympanic is often closely associated during development (MacPhee, 1981).

BASICAPSULAR FENESTRA

synonyms: basicochlear fissure, fissura petrooccipitalis.

"space included between the ventromedial edge of the auditory capsule and the lateral edge of the parachordal cartilage, bounded anteriorly by the anterior basicapsular (or sphenocochlear) commissure, and posteriorly by the basivestibular commissure, or it may be confluent with the foremost part of the fissura metotica, which transmits the glossopharyngeal nerve and is limited behind by the posterior basicapsular commissure." (de Beer, 1937: 399)

CAROTID CANAL

synonyms: none found.

bony canal or tube for the internal carotid artery in basicranial elements ventral and posterior to the passage

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of the internal carotid artery through the internal carotid foramen proper; formed by periosteal outgrowths from the ventral surface of the petrosal in some primates, for example, or by the rostral entotympanic within the bullar wall in most carnivorans.

CHORDA TYMPANI NERVE

synonyms: internal mandibular branch of the facial.

branch of the facial (VII), arising in the tympanic cavity near the facial's exit from the stylomastoid foramen, traveling anteriorly along roof of tympanic cavity, lateral to the stapes, ventrally past the incudomallear articulation, and finally along the inner aspect of Meckel's cartilage, thus exiting via the Glaserian fissure; innervates the tongue (lingual nerve).

COCHLEAR AQUEDUCT

synonyms: aqueductus cochleae, ccchlear canaliculus.

passage in the otic capsule for the perilymphatic (periotic) duct, which runs from the perilymph-filled space within the osseous labyrinth and surrounding the membranous labyrinth of the inner ear to the subarachnoid space; aperture of the duct is on the postercmedial apex of the petrosal, into the emargination at the posterior lacerate foramen.

COCHLEAR FENESTRA

synonyms: fenestra cochleae, fenestra rotunda, round

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window, apertura lateralis of the recessus scalae tympani (de Beer, 1937: 402, 431).

a circular aperture across which stretches the secondary tympanic membrane at the end of the scala tympani portion of the cochlea. not equivalent to the cochlear fossula (q. v.), contra Coombs and Coombs (1982: 227).

COCHLEAR FOSSULA

synonyms: fossula fenestrae cochleae, fossula fenestrae rotundae.

a cavity or funnel-shaped excavation on the ventral or posterolateral surface of the promontorium within which is contained the cochlear fenestra, sometimes hidden from view. A common misconception appears to be that the secondary tympanic membrane is located across the aperture of the fossula rather than at the level of the fenestra contained within it. (MacPhee, 1981: 51, 54)

CONDYLOID CANAL

synonyms: canalis condylaris.

canal within the exoccipital for the occipital venous sinus; anterior opening in the posterior wall of the sigmoid sinus and the posterior opening on the internal surface of the exoccipital, internal to the occipital condyles.

CRISTA PAROTICA

synonyms: crista facialis.

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a process from the posterolateral corner of the petrosal, to which the tympanohyal eventually attaches or fuses, and from which develops the lateral epitympanic wing, the tegmen tympani, from the petrosal.

CRISTA PETROSA

synonyms: petrosal crest.

sharp ridge on the dorsal and anterior surface of the petrosal, extending to the anteromedial apex and forming an edge between the anterolateral face and the dorsomedial face; in forms with a large osseous tentorium, the crista is the medial-most edge of the petrosal's abutment against the tentorium.

CRISTA TYMPANICA

synonyms: crista tympani (Hough, 1953).

a semicircular or circular flange or ridge on the internal face of the ectotympanic ring, forming the medial or dorsomedial wall of the tympanic sulcus (within which attaches the tympanic membrane). (MacPhee, pers. comm.; 1981: 51)

ECTOTYMPANIC BONE

synonyms: tympanic, tympanic ring, annulus tympanicus.

a dermal bone (sensu Patterson, 1977a), circular or semicircular in shape, which supports the tympanic membrane; see Figure 27. Generally considered to be homologous to the reptilian angular. In mammalian

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embryos, this element is horseshoe-shaped, with the opening positioned dorsally in the tympanic notch. It lies almost horizontally across the floor of the tympanic region. The two arms are termed the rostral and caudal horns or legs (e.g. Van der Klaauw, 1931) or the anterior and posterior crura (MacPhee, 1981: 52).

ENTOTYMPANIC BONE

synonyms: endotympanic, metatympanic (Wincza, 1896), os bullae.

Mivart's (1881) term for the independent and presumably neomorphic element(s) in the floor of the tympanic cavity, contributing to the auditory bulla in a variety of forms. Van der Klaauw (1931: 266) included under this term both cartilaginous and ossified elements. In many cases, a rostral ossification center (associated with the tubal cartilage and internal carotid artery) can be distinguished from one or more caudal entotympanics (Van der Klaauw, 1931; Hunt, 1974a).

EPITYMPANIC RECESS

synonyms: recessus epitympanicus, atticus tympanicus (MacPhee, 1981:52).

cavity or excavation in the tegmen tympani (and sometimes partly in the adjacent squamosal), in the roof of the tympanic cavity, housing the incus and head of the malleus. (Sometimes incorrectly used in a much broader

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sense, e.g. Coombs and Coombs, 1982: 226, 227.)

EPITYMPANIC WING

synonyms: none found.

bony or cartilaginous outgrowth into the roof of the tympanic cavity from any of the surrounding bones of the skull.

(OSSEOUS) EXTERNAL AUDITORY MEATUS

synonyms: meatus acusticus externus.

auditory meatus or channel defined usually by the edge of the ectotympanic, sometimes by the petrosal or entotympanic instead (MacPhee, 1981:53). The edges of the ectotympanic may be produced into an OSSEOUS EXTERNAL AUDITORY MEATAL TUBE. The external auditory meatus is continued distally by a cartilaginous portion, which leads into the auricle.

FACIAL CANAL

synonyms: canalis facialis.

an enclosed portion of the facial sulcus on the petrosal, conveying the facial nerve through the tympanic cavity.

FACIAL FORAMEN

synonyms: foramen faciale, apertura tympanica canalis facialis (MacPhee, 1981: 54), secondary facial foramen (Moore, 1981:44).

aperture or foramen, in the tegmen tympani of the

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petrosal, through which the facial nerve (VII) passes from the otic capsule (specifically the cavum supracochleare, housing the ganglion of the facial nerve) into the tympanic cavity of the middle ear. not the foramen stylomastoideum primitivum, although sometimes incorrectly identified as such (see discussion in MacPhee, 1981: 54).

FACIAL SULCUS

synonyms: sulcus facialis, aqueductus Fallopii (Bast and Anson, 1949).

channel in which lies the facial nerve in the middle ear, extending from the facial foramen anteromedially, past the medial side of the crista facialis of the petrosal (site of attachment or fusion of the tympanohyal), and finally to the stylomastoid foramen ventrolaterally. Parts of this sulcus may be roofed over to form a facial canal.

GLASERIAN FISSURE

synonyms: fissura petrotympanica.

fissure between the anterior part of tympanic ring or (in carnivorans, the anterior margin of the rostral entotympanic) and either the posterior wall of the postglenoid process (squamosal) or more medially, the alisphenoid; provides passage early in ontogeny for Meckel's cartilage (Van der Klaauw, 1931: 164), and later for the n. chorda tympani (branch of VII) and accompanying blood vessels, including the inferior ramus of the

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stapedial artery if present. "Glaserian fissure" is an eponymous name, but is still to be preferred over the term most commonly considered synonymous, fissura petrotympanica, because the latter (based on the condition in humans) is not a correct description of the fissure in question in the majority of mammals. In the paleontological literature, the fissura Glaseri is sometimes erroneously described as a notch in the squamosal or postglenoid process, rather than being the fissure itself between the squamosal and the abutting auditory bones (e.g. Coombs and Ccombs, 1982:223). The observed notch in such cases might be the ventral end of a groove for the chordatympani or associated blood vessels (e.g. inferior ramus of the stapedial, etc.) or both.

GLENOID FOSSA

synonyms: fossa mandibularis, mandibular fossa.
concavity in the squamosal bone that receives the articular condyle of the mandible.

HIATUS FACIALIS

synonyms: hiatus fallopii.
aperture at the anterior end of the canal in the petrosal for the greater superficial petrosal nerve (= palatine branch of the facial) which arises from the geniculate ganglion of the VIIth within the petrosal, and joins with the deep petrosal nerve to form the nerve of the pterygoid

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canal (= Vidian nerve). The hiatus facialis is usually positioned at the anterior edge of the petrosal, so that the nerve usually passes ventrally through a foramen in the petrosquamosal or petrosphenoidal suture (or through a persistent piriform fenestra) to the ventral side of the sphenoid. From there the combined nerve of the pterygoid canal exits the auditory region in parallel with the auditory tube and then anterior tc the posterior opening of the pterygoid canal.

HYOID PROCESS

synonyms: processus hyoideus.

tuberosity or rugosity on medial wall of mastoid portion of petrosal bone, to which attaches the tympanohyal cartilage of the hyoid apparatus; part of the crista parotica. The hyoid process is scmetimes incorrectly identified as the "styloid process", which in human anatomy is in the same position, but in the latter represents a fusion of the tympanohyal and stylohyal portions of the hyoid with the petrosal. De Beer (1937: 405) considered it typical for mammals to have the stylohyal fused to this portion of the crista parotica, forming a true styloid process; he notes that it is so fused in Felis (de Beer, 1937: 328). However, this is contradicted by the common observation in the skeleton of the domestic cat of separate hyoid elements that may be identified as stylohyals; these are connected to the skull

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by a cartilage that is considered a cartilaginous tympanohyal, and is contained within the vagina processus hyoideus formed by the entotympanic (see Moore, 1981: 217).

HYPOGLOSSAL FORAMEN OR CANAL

synonyms: canalis hypoglossi, anterior condylar foramen or canal (Jamieson, 1946: 25), trou condylien (Guth, 1964: 34), condylar foramen (Clark and Guensburg, 1972), condyloid foramen (Flower, 1869) or canal (Cooper and Schiller, 1975: 35).

passage through the floor of the braincase, posteromedial to the posterior lacerate foramen, for the exit of the hypoglossal nerve (XII); if elongated into a canal, an intracranial and extracranial aperture of the canal may be recognized. The term "anterior condylar foramen or canal" is used in human anatomy, presumably in contrast to the more posteriorly positioned canal for the occipital sinus, anterior and posterior in humans corresponding to ventral and dorsal respectively of other animals. Guth (1964) reported finding a small vein branching from the occipital sinus passing within the occipital to the hypoglossal canal and exiting via the hypoglossal foramen (his "trou condylien") to join the vertebral vein ventral to the basioccipital.

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HYPOTYMPANIC SINUS

synonyms: none found.

air-filled sinus or chamber enclosed by an inflated bulla ventral to the tympanic cavity in the narrow sense; not particularly distinct from the tympanic cavity and generally included in a broad meaning of "tympanic cavity".

INFERIOR PETROSAL (VENOUS) SINUS

synonyms: sinus petrosus inferior, petrobasilar sinus, sinus petrosus ventralis.

venous sinus lying in a open sulcus sinus petrosi inferioris or within the petrobasilar canal, ventral to the brain, and extending from the cavernous sinus anteriorly to join with the sigmoid sinus posteriorly, thereby forming the internal jugular vein.

INTERNAL AUDITORY MEATUS

synonyms: internal acoustic meatus, meatus acusticus internus.

aperture for the entrance of the acoustic (vestibulocochlear) nerve (VIII) and the facial nerve (VII) into the otic capsule, on the dorsomedial face of the petrosal; in mammals, contains within it at least the primary facial foramen (VII), the superior acoustic foramen (vestibular branch of VIII), and the inferior acoustic foramen (cochlear branch of VIII), although

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additional subdivisions may occur (e.g., see de Beer, 1937: 404-405).

INTERNAL CAROTID ARTERY

synonyms: a. carotis interna, entocarotid artery (but see MacPhee, 1981: 40 for a more general use of "entocarotid").

dorsomedial branch from the common carotid artery, running either medial to or traversing the middle ear cavity, entering the braincase through the anterior carotid foramen, and joining the circle of Willis below the brain. See discussion in text.

INTERNAL CAROTID FORAMEN

synonyms: anterior carotid foramen of some authors, median lacerate foramen of some authors, medial carotid foramen.

passage through the floor of the chondrocranium for the entrance of the internal carotid artery, and the comparable passage through the floor of the ossified cranium. The intracranial orifice of the internal carotid's passage through the ossified cranium is equivalent to the fetal internal carotid foramen, situated next to the sella turcica for the hypophysis (MacPhee, 1981: 40). Depending on relative growth of the basicranial bones, the extracranial aperture of the internal carotid foramen in the adult skull may be

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shifted, often posteriorly. If a bony canal through tympanic elements (as in most carnivorans), or across the ventral surface of the petrosal (as in some primates), is present and at its anterior end co-ossified or closely suturing with the extracranial edge of the internal carotid foramen, the result will be a confluence of that extracranial aperture of the internal carotid with the anterior end of the canal, and often an inability to locate the internal carotid foramen extracranially. See further discussion in text.

MASTOID PROCESS

synonyms: processus mastoideus

rugosity or process for muscle insertion, next to stylomastoid foramen and attachment of the hyoid chain; formed in large part by the mastoid portion of the petrosal (a lateral outgrowth of the crista parotica) and also in varying degrees by the squamosal (whose contribution was termed a post-tympanic process by Van der Klaauw, 1931: 78).

MIDDLE MENINGEAL ARTERY

synonyms: a. meningea media.

branch typically from the first part of the internal maxillary artery, entering cranium via foramen ovale; supplies blood to the meninges of the brain. A common variant is for this artery to become a branch (via

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anastomosis) of the internal carotid artery.

OTIC CAPSULE

synonyms: auditory capsule, capsula otica (MacPhee, 1981: 58).

endocranial chondrification around the organ of equilibrium dorsally, the utricle and semicircular canals (par canalicularis), and around the organ of hearing ventrally, the cochlea (pars cochlearis). The term "auditory capsule" is synonymous with "otic capsule", and neither can be properly used to refer to the fibrous capsule surrounding the inner plus the middle ear. If a term is needed for the latter unit, "tympanic capsule" is probably best since the tympanic cavity is the primary vacuity surrounded.

PAROCCIPITAL PROCESS

synonyms: paramastoid process (Greene, 1935: 16), jugular process (e.g. Field and Taylor, 1950; Crouch, 1969), processus jugularis, exoccipital process (e.g. Jollie, 1962), paracondyloid process (e.g. Walker, 1980).

process of the exoccipital bone posterior to the auditory bulla. It may be closely appressed to the rear wall of the bulla, or entirely distinct.

PETROBASILAR CANAL (Miller et al., 1964: 13, 23; Sisson, 1914: 190).

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synonyms: petrooccipital canal (Getty, 1975: 1470).
canal formed between the petrosal laterally and the medial basicranial elements, the basioccipital and sometimes the basisphenoid, medially; traversed by the inferior petrosal venous sinus. In some taxa it is absent, the sinus being carried in a sulcus on the dorsal surfaces of the basisphenoid, basioccipital, and petrosal. In many forms however, a well defined petrobasilar canal is present, roofed by flanges from the medial bones and the petrosal, and variably floored by similar flanges. Even when a canal is thus formed, because the bony elements contributing to it are not co-ossified, the wall of the canal in each element still forms a channel termed a sulcus sinus petrosi inferioris. I prefer "petrobasilar" to "petrooccipital", because it is specifically the pars basilaris of the occipital that forms one wall of the canal, the anterior part of which may even be a continuation by the basisphenoid.

PETROBASILAR FORAMEN

synonyms: none found.
foramen through which passes the posterior-most section of the inferior petrosal venous sinus, out of the petrobasilar canal to join the sigmoid sinus and thus forming the inferior jugular vein. This foramen is only recognized in those taxa in which a bony partition separates the point of exit of the inferior petrosal sinus

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from the posterior lacerate foramen proper.

PETROSAL BONE

synonyms: petrous portion (pars petrosa) of temporal bone, periotic bone.

dense bone housing the stato-acoustical organs in the inner ear, representing the ossification of the otic capsule (endochondral bone) and derived epitympnic wings (membrane bone, sensu Patterson, 1977a; the epitympanic wing of the petrosal, anteriorly, and the tegmen tympani, laterally); used here to also include the mastoid portion lateral and posterolateral to the otic capsule. See pages 130ff for the rationale for recognizing the petrosal (including the mastoid) as a separate element rather than a part of the "temporal bone."

PIRIFORM FENESTRA

synonyms: pyriform fenestra.

gap between the epitympanic wings of the sphenoid and squamosal bones anteriorly, and the otic capsule or its dorsal outgrowths posteriorly (MacPhee, 1981: 59); large embryonically, but most often closed in adults. The gap that Greene (1935: 16) has labelled the "petrotympanic fissure" in Rattus appears to me to be a persistent piriform fenestra; the former term, however, is usually considered a synonym of fissura Glaseri.

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POSTERIOR CAROTID FORAMEN

synonyms: none found.

orifice through which the internal carotid artery enters the carotid canal if the latter is present; in some taxa, opens into or is apparently confluent with the posterior lacerate foramen.

POSTERIOR LACERATE FORAMEN

synonyms: jugular foramen (but see below), fissura metotica (de Beer, 1937: 431; Moore 1981: 43), incisura jugularis (Nomina Anatomica), foramen lacerum caudale or petrobasilar fissure (Miller et al., 1964: 42).

fissure between the petrosal and basi- and exoccipital bones dorsally and between the latter and the auditory bulla if present, ventrally; traversed by the ninth, tenth and eleventh cranial nerves, and one or more veins. "Jugular foramen" is often used to be synonymous with posterior lacerate foramen, because the inferior petrosal venous sinus (at least in part) and the sigmoid venous sinus usually join to form the internal jugular vein (sometimes called the inferior cerebral vein at this point) either immediately dorsal, within, or ventral to this foramen. However, if a separate petrobasilar foramen is present, then the exits of the sigmoid sinus (usually via the posterior lacerate foramen) and the inferior petrosal sinus are necessarily separate. In this case,

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the internal jugular is clearly not traversing this aperture, and the term "jugular foramen" becomes a misnomer. The descriptive implications of either "posterior lacerate foramen" or "metotic fissure" are apparently never violated; the former is in more common use in the paleontological and comparative anatomical literature.

POSTGLENOID FORAMEN

synonyms: retroglenoid foramen, retroarticular foramen, foramen petrosquamosa (Swindler and Wood, 1973: 6).

foramen posterior to glenoid fossa, conveying superior petrosal venous sinus, transverse venous sinus, or confluence of two, to external jugular drainage; variably present, and when present, variably positioned anywhere from anterior to bulla (i.e., placed rather medially) to positioned far laterally and posteriorly (in suprameatal shelf) in squamosal bone.

POSTGLENOID PROCESS

synonyms: retroglenoid process, retroarticular process.

projection of the posterior margin of the glenoid fossa, extending ventrally and often curving around the articular condyle of the mandible (McDowell, 1958: 127; MacPhee, 1981:60).

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PROMONTORIUM

synonyms: none found.

the low, rounded, ventral projection of the pars cochlearis of the petrosal, into the tympanic cavity.

PTERYGOID CANAL

synonyms: canalis pterygoideus, Vidian canal.

canal usually between the pterygoid and basisphenoid bones; transmits a nerve that is a combination of the greater superficial petrosal nerve (issuing from the petrosal via the hiatus facialis (q.v.)) and the deep petrosal nerve (n. petrosus profundus). There is also sometimes present in this canal an accompanying artery that is a small intratympanic branch of the internal carotid artery, at least embryonically (may be captured by the external carotid system later; MacPhee, 1981: 47). A groove (sulcus nervi pterygoidei) is frequently present on the basisphenoid, running from the auditory region to the posterior opening of the canal.

SEPTUM BULLAE

synonyms: none found.

bony septum in the auditory bullae dividing the hypotympanic sinus into two spaces; restricted by Hunt (1974a), following Winzca's (1896) original use of the term for the septum in the cat, to a specifically bilaminar septum composed of inturned edges from both

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ectotympanic and caudal entotympanic bones.

SIGMOID (VENOUS) SINUS

synonyms: sinus sigmoideus, posterior portion of the transverse sinus.

venous sinus of the dura mater connecting the superior petrosal sinus and the transverse sinus dorsally with the inferior petrosal sinus ventrally to form the internal jugular vein; contained within the sigmoid sulcus (immediately posterior to the endochondral petrosal) in the posterodorsal (mastoid) wing of the petrosal and in the exoccipital.

SPHENORBITAL FORAMEN

synonyms: fissura orbitalis superior, orbital fissure, sphenoidal fissure, anterior lacerate foramen.

large aperture in the suture between the alisphenoid and orbitosphenoid bones in the orbital fossa, providing passage for at least four nerves (oculomotor III, trochlear IV, abducens VI, ophthalamic division of trigeminal V, and in some cases the optic nerve tract II, as well), the internal ophthalmic artery from the internal carotid artery, and a vein from the cavernous sinus to the vena reflexa.

STAPEDIAL ARTERY

synonyms: pterygopalatine artery (Greene, 1935: 183).

lateral branch, from the internal carotid artery, which

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runs through the tympanic cavity, specifically perforating the stapes; primitively large in tetrapods, supplying through supraorbital, infraorbital, and mandibular branches, the mandible, upper jaw, and contents of the orbit excluding the eyeball; in many eutherians, anterior portions of this supply are taken over by the external carotid system via large anastomotic channels, and the stem of the stapedial is either greatly reduced or lost.

STYLIFORM PROCESS

synonyms: "styloid process" (e.g. Cooper and Schiller, 1975; not the styloid process of the petrosal--see hycid process, above), "muscular process of the temporal bone" (Bradley and Grahame, 1943: 213), muscular process (Miller et al., 1964).

anteromedially directed projection from the ventral margin of the tubal foramen, at the anterior edge of the auditory bulla, lateral to the anteromedial process of the bulla if the latter is present; site of origin of the muscularis levator veli palatini.

STYLOMASTOID FORAMEN

synonyms: foramen stylomastoideum, tertiary facial foramen (Moore, 1981: 46).

foramen through which the facial nerve (VII) exits the tympanic cavity, surrounded by either entotympanic or

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mastoid or both, and adjacent (lateral) to the hyoid process. This foramen is sometimes termed the foramen stylomastoideum definitivum to distinguish it from the foramen stylomastoideum primitivum, the aperture formed by the passage of the facial nerve through the basilar membrane flooring the tympanic cavity prior in ontogeny to the formation of the bulla.

SUBARCUATE FOSSA

synonyms: fossa subarcuata, parafloccular fossa, cerebellar fossa, appendicular fossa (Reighard et al., 1935: 58; Booth, 1948: 9).

concavity in dorsomedial (intracranial) face of petrosal to accomodate the paraflocculus of the cerebellum; rim of subarcuate fossa is formed by the swelling of bone around the superior semicircular canal.

SUPERIOR PETROSAL (VENOUS) SINUS

synonyms: sinus petrosus superior, sinus petrosis dorsalis.

venous sinus carried by sulcus or canal within the squamosal bone along the dorsal margin of the petrosal, exiting anteriorly via the postglenoid foramen if one is present, confluent anteriorly with the cavernous sinus ventrally, and posteriorly joining with the transverse sinus to form the sigmoid sinus.

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SUPRAMEATAL FOSSA

synonyms: none found.

excavation in the squamosal bone dorsolateral to the tympanic membrane, communicating with the epitympanic recess within the tympanic cavity (Tedford, 1976: 366); characteristic of at least procyonids and perhaps primitively of all arctoids.

TEGMEN TYMPANI

synonyms: none found.

initially posterolaterally and ventrally directed ledge from the otic capsule, which subsequently grows anteriorly, roofing over the epitympanic recess; a mammalian feature, derived from the crista parotica.

(OSSEOUS) TENTORIUM CEREBELLI

synonyms: none found.

bony plate extending out from walls and down from roof of cranial cavity, partly separating the cerebral and cerebellar portions of the cavity; lateral portion closely appressed to dorsolateral face of petrosal in many taxa.

TYMPANIC CAPSULE

synonyms: none found.

term proposed here for the unit comprising the ossifying otic capsule, auditory ossicles, tympanic membrane, auditory tubal cartilage, ectotympanic, fibrous flooring membrane, tympanic cavity, and enclosed nerves and blood

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vessels.

TYMPANIC CAVITY

synonyms: cavitas tympanica, cavum tympani.

air-filled space enclosed by the auditory bulla, or the fibrous membrane flooring the tympanic region; contains the tissues and structures cf the middle ear. A strict definition of the tympanic cavity includes only the space immediately around the ossicles, vestibular fenestra, and cochlear fossula, extending ventrally as far as the fetal position of the fibrous membrane flooring the middle ear. The space enclosed by expansion of the bulla beyond this basic position is termed the "hypotympanic sinus". Because these two spaces are so pcorly demarcated, I use tympanic cavity in this study in the general, inclusive sense; if necessary, one could refer to the cavum tympani primitivum, since its demarcation is primarily on the basis of embryonic structure.

TYMPANIC MEMBRANE

synonyms: tympanum, eardrum.

membrane stretched across the ectctympanic ring, separating the external and middle ear cavities; functions in conducting sound vibrations from air to ossicular chain; comprises two parts, the pars tensa (which inserts in the tympanic sulcus of the ectotympanic) and the pars flaccida (thin, membranous, dorsal extension between the

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malleus and the dorsal rim of the osseous external auditory meatus). The former is the part that directly transmits sound to the malleus, and the latter an extensible section that partially determines the effective volume of the middle ear (Fleischer, 1978).

TYMPANIC NOTCH

synonyms: incisura tympanica, notch of Rivinus (MacPhee, 1981:65).

notch formed by the postglenoid process and margin of the glenoid fossa anteriorly, and the mastoid process posteriorly, through which extends the external auditory meatal tube.

TYMPANIC RING

synonyms: none found.

that portion of the ectotympanic comprising the crista tympanica, the tympanic sulcus, and the osseous external meatus; equivalent to the ontogenetically early form of the ectotympanic, primitively horseshoe-shaped rather than a complete ring.

TYMPANIC SULCUS

synonyms: none found.

groove on inner surface of ectotympanic ring, into which inserts the tympanic membrane.

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VAGINA PROCESSUS HYOIDEUS

synonyms: none found.

deep pit formed by bone of the osseous auditory bulla surrounding the (usually cartilaginous) tympanohyal at its articulation with the hyoid process of the petrosal, immediately adjacent to the stylomastoid foramen.

VESTIBULAR AQUEDUCT

synonyms: aqueductus vestibuli.

passage in the otic capsule for the endolymphatic (otic) duct, which runs from the endolymph-filled utriculus and sacculus of the membranous semicircular canals to the endolymphatic sac, lodged in the slit-like posterior portion of the aqueductus vestibuli and projecting in beween two layers of the dura mater.

VESTIBULAR FENESTRA

synonyms: oval window, fenestra ovalis.

oval aperture in the lateral wall of the petrosal, across which is positioned the footplate of the stapes and the annular ligament.

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MORPHOLOGICAL DESCRIPTION: NIMRAVIDAE

The best preserved and most plentiful nimravid material in North America is currently referred to the genus Dinictis--a medium-sized catlike carnivoran that, although clearly a nimravid, is in some ways the least modified of the group. Although the degree of sabertoothy was perhaps slightly greater in Dinictis than in Nimravus, members of the latter genus show several features apparently autapomorphic for Nimravus. We are fortunate in this circumstance, because the result is that the several excellent specimens of Dinictis provide examples of character states perhaps derived for the family but primitive within it, and thus more likely to be transitional between the nimravids and their closest relatives. (I am not suggesting that the possession of a character state by Dinictis is therefore evidence that that character state is primitive. I am only observing that Dinictis has many features that on other grounds I consider primitive at a fairly general level within this analysis.)

Since Dinictis is known most completely, the following description of its basicranial morphology is the most detailed and most extensive. The subsequent descriptions do not repeat all of the explanatory details when those would be repetitive of the explanations already

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provided in the description of Dinictis.

For each description, the material examined is briefly listed at the beginning, with the following annotations:

l = left ear region prepared and studied

r = right ear region prepared and studied

internal = intracranial surfaces were prepared and studied

On several of the skulls, both ear regions are present but only one side has been adequately prepared.

DINICTIS

Based in detail on AMNH 455 (l) [type of Dinictis felina Leidy], AMNH 6937 (r) [type of D. cyclops Cope], AMNH 8777 (l & r), F:AM 62034 (l & r), F:AM 104823 (l & r), AMNH SD 230-4152 (l, r & internal), ANSP 12547 (l), USNM 15889 (l), and YPM 20268 (l).

Tympanic Floor: Auditory Bulla

Ectotympanic.--The ectotympanic in Dinictis is a gently curved plate of bone on the lateral and anterolateral surfaces of the auditory area. Its anterior and posterior crura are elongate, but do not meet dorsally, thus leaving a gap of three to four millimeters

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just medial to the roof of the tympanic notch. The plane of the tympanic ring is very nearly vertical in adults (e.g. AMNH 6937 and 455), and oriented approximately 30 degrees from the sagittal plane. This appears to be the case even in those specimens Hough (1953) studied (AMNH 8777, 6937, and USNM 15889), contrary to Hough's description: removal of additional matrix from within the external auditory meatus of each revealed large anterolaterally facing meati, facing almost as far anteriorly as did the external auditory meatus in Hoplophoneus. Subadult individuals (F:AM 104823 and USNM 15889) show the greater inclination from the vertical typical of the tympanic ring in young carnivorans generally.

The plane defined by the bony edge of the external auditory meatus is roughly parallel with the plane defined by the edge of the crista tympanica: the crista is little produced into the tympanic cavity, evenly extending approximately a millimeter medially from the main plate of the ectotympanic. There is thus no extension of the hypotympanic sinus into the osseous meatus ventral to the crista as is found in ursids and otariids. A fairly large, almost complete circle is formed by the crista tympanica, which extends onto both the anterior and posterior crura of the ectotympanic.

Instead of an osseous external auditory meatal tube,

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there is a large oval osseous meatus, wider than the tympanic notch in the squamosal. Two of the above features in combination--the orientation of the tympanic ring and meatus, and the relatively large size of the meatus--result in a positioning of the auditory meatus medial to the postglenoid process as well as medial to the tympanic notch. This is a surprisingly anterior position for the tympanic ring.

The anterior crus of the tympanic ring does not fuse with the squamosal; instead, it rests in a shallow depression posteromedial and slightly dorsal to the postglenoid foramen. The end of the anterior crus is broadened, with a thick, blunt processus tubarius extending dorsomedially along the anterior edge of the epitympanic recess.

No corresponding broadening of the posterior crus is seen. In those specimens in which the tympanic ring is complete and this area well preserved (AMNH 6937 and F:AM 104823), the posterior crus can be seen to lie along the lateral half of the hyoid process of the mastoid (the fused tympanohyal), resting in a shallow concavity in the anterior face of the base of the mastoid process. In only AMNH 6937 does the posterior crus appear to be both complete and in place. In AMNH 455, the dorsal tip of the posterior crus is broken off, and in F:AM 104823, the posterior part of the ectotympanic appears to be displaced

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ventrally and medially, with the result in both cases that the shallow concavity in the squamosal is visible.

The ectotympanic is medially expanded anteriorly, slightly medially expanded ventrally, but not at all expanded posteriorly. In Dinictis cyclops (AMNH 6937), in which the ectotympanic appears to be complete, the ventral margin at its posterior end bears a roughly pyramidal process, with a roughened surface ventromedially. This portion of the ectotympanic is positioned just anterior to the point of attachment of the hycid apparatus. In contrast, F:AM 104823 and AMNH 8777, which also appear to possess relatively complete ectotympanics, display a slight broadening of the ventral margin posteriorly, but a relatively smooth curve anterior to the processus hyoideus, without the ventral extension seen in D. cyclops.

Broadening of the ventral edge of the ectotympanic, combined with either a rugosity of the edge's surface (AMNH 6937 and F:AM 104823) or a pitting or channeling of the surface (AMNH 6937 and 8777), argues that the margin of the ectotympanic represents the limits of ossification of the bone in these three specimens. This margin is easily distinguished from a broken edge, resembling in its shape and texture the edge of the ectotympanic in Nandinia that abuts the cartilaginous entotympanic. (Nandinia differs in that the anterior inflation of the ectotympanic

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is greater, resembling the other aeluroids, and the dorsal edge of the entotympanic margin is more produced into a sharp flange, which may be interpreted as the remnant of the septum bullae.) Broadening of the ventral margin is greatest posteriorly, near the attachment of the hyoid apparatus, and tapers anteriorly.

Expansion of the ectotympanic extends anteromedially (but not ventrally as in aeluroids), well beyond the tympanic ring, forming the anterolateral margin of the bulla and a bony trough for the auditory tube. The ventral edge of this anterolateral wall is emarginate, either greatly so as in ANSP 12547, AMNH 6937 and 8777, or with a small, very anteriorly placed notch, as in USNM 15889 (right side). This section of the ectotympanic is very little produced dorsally: only a narrow anterodorsal shelf lies against the epitympanic wing of the alisphenoid. In the most complete specimen, AMNH 6937, a process of the ectotympanic extends ventrally, below the anterior end of the trough for the auditory tube. The medial side of the trough in AMNH 6937 is low and lies appressed to a lip of entotympanic. This relationship is described in more detail below.

Hough's (1953: 103) statement that the ectotympanic in USNM 15889 is in contact with the basisphenoid is incorrect, except possibly to the extent that the auditory tube, were it present, would be overlain by

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sphenoid--probably alisphenoid, however. Her inference that the ectotympanic portion of the bulla extended to the medial side of the auditory region was perhaps based on a misinterpretation of some matrix in that specimen. In no specimen of Dinictis that I have seen, including USNM 15889, does the ectotympanic extend to the medial margin of the bulla. Instead, in the most complete specimen, AMNH 6937, the anteromedial corner of the entotympanic extends to the anterior margin of the bulla. In USNM 15889, although the anterior parts of the entotympanic are not present, the anterior ends of the medial margins of the ectotympanics appear to be complete on both sides: they are roughly the same semicircular shape anteriorly, and posteriorly are clearly broken. I therefore doubt if Hough saw bone extending to the basisphenoid (I do not think any has broken off from this region subsequent to her study), but think rather that she mistook shellacked matrix in that region for bone. Certainly ANSP 12547 appears to have a complete anterior half of the left ectotympanic, and again, there is no indication that the ectotympanic abutted the basisphenoid medially. Instead the medial wall (at least dorsally) of the canalis musculotubarius would have been formed by entotympanic.

No clear styliform process is usually present, unless the broken anterior end of the ectotympanic in AMNH 8777 bore one; the ventrally directed process from the bottom

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of the auditory tube in AMNH 6937 is in the right position but the wrong orientation tc be equivalent to the styliform process of modern carnivorans. In ANSP 12547, however, the semicircular shieldlike portion is bounded anteriorly by a large emargination on the medial edge, with smooth edges; the anterior limb of the bone around this emargination projects anteromedially and somewhat ventrally in a long, thin pointed process ventral to the passage for the cartilage of the auditory tube. Like the hamular processes of the pterygoid, a long thin styliform process of this sort would frequently be broken off.

Entotympanic.--Ossified portions of entotympanics are present in numerous specimens. In no specimen of Dinictis found to date (and known to me) is a complete and fully ossified bulla present.

Hough (1953: 105) interpreted a supposed cast of the interior of the bulla in AMNH 6937 to be evidence that the bulla was originally completely ossified. (The catalogue number given in her publication is AMNH 6930, but this number is that of a specimen of Nimravus; she did say here that she was referring to the type of Dinictis cyclops, which is AMNH 6937 and does have the most complete bulla I have yet observed in any non-barbcurofeline nimravid.) A complete cast of the tympanic cavity was not observed in AMNH 6937 prior to its preparation for this study: matrix filled the ear region to the level of the remaining

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entotympanic, but was leveled off and did not present the appearance of a cast, nor was there any sign of preparation attempts prior to our preparation. Even if a rounded cast has been preserved in some specimen, it could be equally convincingly interpreted as evidence that the floor was cartilaginous since the region filled with matrix but the entire floor is never preserved. In the left auditory region of ANSP 12547, for example, much of the remaining matrix appears to retain the shape of the bulla, although sections of the cast have evidently been removed by preparation at some time. In the ventral surface of the remaining part of the cast, there are no traces of bone preserved.

Hough (1953: 103) inferred that "the bulla in Dinictis must have been very large and well inflated." The same three specimens that she examined, AMNH 8777, 6937, and USNM 15889, appear to me to present a slightly different condition, even when compared to Canis as she did. The nearly vertical angle of the ectotympanic and entotympanic demonstrates indeed that the bulla was not flattened, but rather was inflated ventrally. However, given a normal amount of ventral extent, I would not call the bullae particularly large relative to the overall size of the basicranium, especially when one considers that it does not in a sense "fill" the available space. Compared with the bulla in Canis latrans, the following differences

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in extent become apparent: the ectotympanic in Dinictis is not pushed up against the postglenoid process or posterior face of the squamosal. Medially the basioccipital is indeed compressed, but the petrosal extends medially and somewhat ventrally (although not nearly to the extent seen in many aeluroids) and the medial part of the entotympanic is thick so the tympanic cavity is further restricted. Posterolaterally, the bulla is far from the edge of the skull (contra Hough, 1953: 103). Instead there is a broad shelf or crest uniting the paroccipital and mastoid processes (much like that seen in mustelids), so that the skull extends laterally well beyond the bullae. The tympanic cavity extends only slightly, if at all, posterior to the promontorium.

All preserved entotympanics display a very unusual condition: they are thick structures throughout, tapering to a thin edge only at their dorsal edges, which lie against the promontorium. Both dorsal and ventral surfaces of entotympanic are paper-thin layers of bone (e.g., left side of F:AM 62034), easily damaged in preparation and frequently badly gouged in hastily prepared specimens. Sandwiched between these two thin layers is a much thicker layer of cancellous bone, irregularly honeycombed. Broken ventral edges of the entotympanics in AMNH 6937, 455, F:AM 62034, and especially YPM 20268 show this structure clearly in cross

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section. F:AM 104823 presents, in contrast, entotympanics with unbroken ventral margins: they are a smooth trough, as shown in Figure 28. (In none of these specimens did a broken edge of ectotympanic display this cancellous interior and thin surface skin of bone; all ectotympanics appeared to be normal, solid bone.)

Although the entotympanic is clearly incomplete in most specimens (e.g. F:AM 62034 and AMNH 455) and sometimes, although very nearly complete, obviously displaced from its natural position (e.g. F:AM 104823), in very rare specimens the entotympanic is not only in situ but, by its relationships with the ectotympanic, presents the appearance of being the complete extent of the ossified portion of that element, anteriorly and posteriorly (e.g. AMNH 6937 (r)), and even at the ventral edges (e.g. AMNH 104823). Here, ossified entotympanic is present in a complete semicircle from the posterolateral quadrat to the anteromedial corner of the auditory region. Its dorsal margin overlaps a small margin of the promontorium posteriorly and posteromedially, just abuts the petrosal in the middle of its medial margin, and extends laterally to overlap a small margin of the promontorium again anteromedially. The expanded, shallow, dish-shaped anterior portion is overlain by the epitympanic wing of the alisphenoid.

In AMNH 6937, the anterior margin of the entotympanic

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is ossified ventrally to the level of the projection from the ectotympanic trough for the auditory tube. This part of the entotympanic curves posterclaterally to end in a finished edge projecting into the anterior half of the tympanic cavity and forming a curve continuous ventrally with the ventral edge of the ectotympanic. From the medial side, this wall appears somewhat like the partial septum in canids, as emphasized by Brunet (1967). However, this ridge does differ from the longer septum in Canis: although the portion of the tympanic cavity on the medial side of this ridge (walled by the inflated entotympanic) is large, the tympanic cavity extends little if at all past the ridge on the lateral side. Instead the well defined osseous channel in the ectotympanic for the auditory tube begins immediately, so that the entotympanic wall actually represents a dorsal separation between the tympanic cavity and the auditory tube.

AMNH 6937 (Figure 29) shows clearly the details of the relationship between the anterior ends of the ectotympanic and entotympanic, summarized in the diagrams in Figure 30. A thickening and lateral expansion of the entotympanic fits into the emargination of the ectotympanic at the ventral end of the anterolateral entotympanic wall. No fusion or interfingering at the ectotympanic/entotympanic contact is visible, leaving the line of demarcation between the two elements very

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distinct.

The question of the presence of a septum in the auditory bulla of any nimravid is an important one because of the emphasis placed on septa in phylogenetic hypotheses for the Carnivora. As described above, the anterior margin of the entotympanic curves inward in a fashion faintly resembling the larger partial septum of canids, but without the accompanying inflation of the adjacent ectotympanic portion of the bulla. This condition in no way matches Scott's (1889: 214) assertion that the bullae were "almost certainly divided by an internal septum into two chambers"; the rest of his discussion (ibid., p. 214) makes it clear that he did not actually observe a septum, nor any direct evidence for one.

The canal for the pterygoid nerve is very distinct in the sphenoid roof at the anterior end of and medial to the canalis musculotubarius. It appears to come from a small foramen between the squamosal (or sphenoid--the position of the suture is not evident) and the petrosal at the anteromedial-most corner of the fossa muscularis major. Although it is very difficult to see far into the canalis musculotubarius, there appears to be a small, matrix-filled aperture, located between the entotympanic septum and the ectotympanic ridge on the lateral side of the canalis musculotubarius. This I take to be the ventral opening for an anastomotic ramus from the

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ascending pharyngeal artery, or for whatever traveled along that channel in the basisphenoid beneath the anterior portion of the entotympanic, paralleling the canalis musculotubarius.

Various cross sections of the medial section of the entotympanic (especially F:AM 104823) demonstrate the absence of any grooves or canals posterior to the internal carotid foramen for a medially placed internal carotid artery.

Posteriorly, the entotympanic curves around the wall of the excavation for the auditory chamber, lying against facets on the basioccipital, exoccipital, and mastoid elements, and meeting the ectotympanic anteromedially to the facial canal. In AMNH 6937 and YPM 20268, the entotympanic appears to form the medial and posterior margins of the stylomastoid foramen, while the mastoid forms the lateral margin, and the processus hyoideus forms the anterior margin. However, in AMNH 455, F:AM 62034 and 104823, in which the posterolateral portion of the entotympanic is absent, a distinct caudal process of the petrosal is evident, extending to and fusing with the base of the mastoid process in the posterior wall of the facial sulcus (leaving a foramen for the auricular branch of the vagus nerve, especially clear in AMNH 455). The caudal process of the petrosal also projects anteriorly, forming part of a medial wall to the facial sulcus, very nearly

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contacting the processus hyoideus and thus forming a nearly closed canal for the facial nerve. The process is flattened ventrally, in continuity with the posterior shelf on the petrosal, as if it were underlain closely by the dorsal lip of the entotympanic. Re-examination at this point of AMNH 6937 opens the possibility that the entotympanic present in the posterolateral corner is lying appressed to the caudal process of the petrosal (which is thus just barely visible ventrally) and it is the latter that forms the medial and posterior margins of the ventral end of the facial canal. Of course, more ossified entotympanic may have been present in life ventral to that observed now, so that the foramen stylomastoideum definitivum was probably bounded at least in part by entotympanic.

I initially interpreted the position of the entotympanics on both sides of F:AM 104823 as being the result of displacement, although they also appear to be somewhat less inflated in this juvenile or young adult than in the fully adult AMNH 6937. It is of note, however, that the other specimen in which the entotympanic is some distance from the basioccipital flange instead of being appressed to it is a juvenile Nimravus (F:AM 99259). Two possibilities are suggested: either the entotympanic was less firmly anchored in juveniles and therefore easily displaced away from the basioccipital wall during

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preservation (the similarity in the displacement in these two specimens being more or less coincidental) or the observed gap represents the original condition and was closed in the course of ontogeny by continued inflation of the entotympanic part of the bulla.

Facets on the bones forming the posterior margin of the auditory cavity are clearly visible in all specimens, indicating the extent of the entotympanic. In only AMNH 6937 is the entotympanic complete enough posterolaterally to display a well-defined posterior carotid foramen through the posterior wall of the entotympanic. This foramen is positioned quite laterally, very nearly to the level of the aperture of the cochlear fossula, and dorsal to the ventral margin of the exoccipital, almost as far dorsal as the bottom of the promontorium. On the left side of F:AM 104823, a groove across the posterior wall of the entotympanic may represent the roof of the posterior carotid foramen in this specimen.

Tympanic Roof

The auditory region of Dinictis is moderately deeply excavated: the ventral-most edges of the basioccipital, basisphenoid, squamosal, and mastoid all extend quite far below the dorsal roof of the tympanic cavity. Hough (1953: 103) stated that "the auditory cavity proper is shallow, as is usual in dinictids, and in contrast to

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Hoplophoneus". While it is true that the auditory region in Hoplophoneus is even deeper relative to its length and width, the auditory cavity of Dinictis is in fact deeper than is usual for carnivorans.

Petrosal.--The moderately large, rounded promontorium is flanked by a shelf posteriorly which overlies the entotympanic, and laterally and anteriorly by the tegmen tympani and the epitympanic wing of the petrosal. As can be seen in Figure 31, the petrosal has a broad contact posteromedially with the basioccipital, and posteriorly and posterolaterally with the exoccipital and mastoid. The margin of the posterior shelf is notched by the posterior lacerate foramen, and in most specimens is incised by a deeper notch, presumably for the tympanic nerve. A lateral portion of the caudal process of the petrosal is present, posterior and medial to the facial canal. This process extends ventrally anterior to the lateral-most extension of the entotympanic, between the entotympanic and the mastoid. Thus, between the petrosal and the mastoid, the process forms a bridge or transverse wall, the posterior wall of the facial sulcus as it turns ventrally to course along the median face of the mastoid. However, the wall formed by the caudal process of the petrosal is more deeply excavated than appears necessary for the facial nerve alone, especially in AMNH 455 and F:AM 62034: the fossa immediately lateral to the aperture

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of the cochlear fossula, and posteromedial to the facial sulcus may be the fossa muscularis minor, the site of insertion of the stapedius muscle.

The aperture of the cochlear fossula is directed posterolaterally and somewhat ventrally. There is a pronounced bulge in the promontorium ventral to the aperture, accentuated by a shallow depression or channel, on the posterior side of the promontorium, extending medially from the medial margin of the aperture of the cochlear fossula. In contrast to Hough's implication that the position of the cochlear fossula is odd in Dinictis (and has a special similarity thereby to Daphoenus), I have found the position in Dinictis to be the typical position of the cochlear fossula in all carnivorans examined.

One or two small grooves are frequently present on the lateral half of the promontorium, oriented roughly anteroposteriorly (longitudinally).

A large and well defined facial sulcus courses across the ventral surface of the tegmen tympani, just lateral to the aperture of the cochlear fossula, and anteriorly, lateral to the anterolaterally directed vestibular fenestra. Dorsal to the vestibular fenestra, the channel turns mediad. Its subsequent course shows variation in the degree to which it is floored as well as roofed by petrosal. The typical mammalian condition may be seen in

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AMNH 455: the sulcus is confluent with a foramen in the epitympanic wing of the petrosal directly anterodorsal to the vestibular fenestra. In other specimens, the sulcus is open ventrally for a longer extent medially. F:AM 62034, for example, exhibits an open groove along nearly the entire anterodorsal margin of the promontorium, terminating in a facial foramen positioned near the medial edge of the epitympanic wing of the petrosal. F:AM 104823 displays an intermediate condition: a bridge of bone is present forming a foramen in the appropriate position, but the channel opens again ventrally immediately, so that an open groove is present, and the final foramen is again more medially placed.

The petrosal extends in an epitympanic wing rostrally, meeting the epitympanic wings of the squamosal and alisphenoid and thus largely obliterating the piriform fenestra. Excavated within this epitympanic wing of the petrosal is a well defined fossa muscularis major for the tensor tympani muscle. In some specimens (e.g. AMNH 455 and F:AM 104823), the anterolateral border of this fossa is well defined by a sharp ridge or shelf of bone; in others this is less well developed or not preserved. On the ridge of bone between the fossa muscularis major and the epitympanic recess, anterior to the facial foramen, there occasionally is visible a very small foramen opening dorsally into the epitympanic wing of the petrosal.

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The epitympanic recess is about the same size as the fossa muscularis major, positioned lateral to it, and roofed by both the epitympanic wing of the petrosal and the squamosal. The suture between these two elements is clearly evident. In very well cleaned specimens missing enough of the ectotympanic to permit an unobstructed view of the epitympanic recess (AMNH 455 and F:AM 62034), there is a small foramen on the suture or just ventral to it in the squamosal. Although the foramen appears to be directed posteromedially in F:AM 62034, its size and position are otherwise appropriate for a superior ramus of a stapedial artery (see below). A secondary small pocket is deeply excavated in the petrosal portion of the epitympanic recess for the posterior crus of the incus. A small foramen is variably present on the medial margin of this pocket, dorsal to the facial sulcus (F:AM 104823), or present on the medial margin of the epitympanic recess, caudal to the deeper pocket and on the edge of the facial sulcus (F:AM 62034).

Sphenoid.--The alisphenoid, basisphenoid, or both develop an epitympanic wing that extends caudally to contact the epitympanic wing of the petrosal. I have not found any specimen in which I can identify the condition described by Hough (1953: 103), in which the anterior part of the tympanic cavity is "roofed by an extension of the alisphenoid that meets the basisphenoid laterally and is

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in contact with the promontorium by a narrow process." I cannot determine the position of a suture between basisphenoid and alisphenoid, except possibly along the medial side of the canal for the pterygoid nerve. (See Figure 31.) A diagonal channel in the sphenoid represents the dorsal roof of the osseous auditory tube. Along the medial side of the epitympanic wing of the sphenoid in F:AM 62034, next to the rugose area of attachment of the entotympanic, a smooth, well defined channel runs anteroventrally from the internal carotid foramen (here the widened anterior end of the basicapsular fissure, the sphenocochlear commissure have apparently failed to ossify) to the anteromedial corner of the bulla (as shown in Figure 32). This channel is underlain by entotympanic (as seen in the left ear region of F:AM 62034) and perhaps gave passage to an anastomotic branch from the ascending pharyngeal artery to the internal carotid foramen.

Hough (1953) described the presence of a piriform fenestra in Dinictis, implying that it was observed in AMNH 8777 and USNM 15889. However, neither of these specimens was prepared thoroughly enough to observe the condition of the piriform fenestra. In those specimens in which the tympanic roof is completely visible, the sphenoid meets the petrosal broadly, not "by a narrow process" (ibid., p. 103), and the piriform fenestra is almost completely closed, as indeed Hough reported for

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USNM 16558, although a remnant of the fenestra persists immediately anteromedial to the fossa muscularis major.

Squamosal.--Lateral to the alisphenoid, the squamosal continues the anterodorsal wall of the auditory region. A prominent postglenoid process and slightly pedestalled glenoid fossa contribute to the relative depth of the auditory cavity. The slight depression posteromedial to the postglenoid foramen receives the anterior crus of the tympanic ring. On the anterior face of the mastoid process, in the squamosal portion of that structure, another shallow concavity looks like a very reduced suprameatal fossa in specimens with the ectotympanic missing or displaced, and was reported to be a suprameatal fossa by both Hough (1953) and Brunet (1967), but proves to be the comparable concavity for the posterior crus of the ectotympanic, as demonstrated by AMNH 6937. (Compare the shallow concavity in Dinictis in Figure 31 with the deep and well defined suprameatal fossa in Nasua in Figure 23.)

Principal Tympanic Spaces and Foramina

The total volume actually enclosed by ecto- and entotympanics seems disproportionately small for the size of the skull, primarily because the entotympanic is not cupped by the surrounding elements, except slightly by the basisphenoid and basioccipital. This failure of the

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bullar inflation to invade the occipital or mastoid results in a bulla that seems small relative to the size of the basicranium. However, the auditory region in Dinictis is fairly deep: nearly vertical entotympanic walls appear to circumscribe a large hypotympanic space relative to the horizontal dimensions of the bulla. Its position is also remarkably far forward, so the anterior end of the bulla is medial to the glenoid fossa for the mandibular articulation.

Tympanic cavity.--Both the flatness (lack of inflation) of the ectotympanic and its lack of expansion medially contribute to the narrowness of the tympanic cavity proper (contrary to Hough's, 1953: 106, observations and interpretations). The roof of the tympanic cavity is quite recessed, so the cavity extends well dorsal to the level of the promontorium (which is itself placed slightly dorsally).

Epitympanic recess.--This concavity is remarkably shallow, but contains in the part roofed by the petrosal a deeper pocket to receive the posterior crus of the incus and the attachment of the suspensory ligament.

Within the squamosal section of the epitympanic recess there is a small but very distinct foramen, observable in F:AM 62034 and AMNH 455. The foramen may be at the suture between the squamosal and petrosal, as in the former, or entirely within the squamosal, as in the

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latter, but in either case just lateral and ventral to the deep secondary pocket within the recess. This foramen is in an appropriate position to have carried the superior ramus of the stapedial artery, although the apparent posteriorly directed orientation of the foramen in F:AM 62034 is unusual for a foramen conducting that blood vessel. (This artery is absent in the adults of all carnivorans as far as is known; the problem is discussed further below.)

Posterior lacerate foramen and adjacent foramina.--The posterior lacerate foramen is situated quite laterally, in the center of the posterior margin of the auditory region rather than at the posteromedial corner. It is presumed to have conducted the vein from the sigmoid sulcus, which ends at its lateral edge, and nerves IX, X, XI. In specimens with the posterior wall of the bulla at least partly intact, the external opening of this foramen is defined posteriorly by a broad notch in the occipital and anteriorly by the smooth wall of the entotympanic. Absence of the entotympanic in this region reveals the dorsal continuation of the channel in the occipital through to its dorsal surface and a corresponding notch in the posterior margin of the petrosal, defining the internal portion of the posterior lacerate foramen. A distinct, narrow notch in the center of the broader emargination of the petrosal is frequently

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present and would have conducted the tympanic nerve ventrally into the ear region between the dorsal lip of the entotympanic and the promontorium.

Some variation is observable in the degree to which the hypoglossal foramen is close to or associated with the posterior lacerate, but in no case are they ever confluent as is often the case in the Felidae. The bridge of occipital separating the two is always clearly visible, close to the external surface, and often extending more ventrally than any ridges that may appear to tie the hypoglossal foramen to the posterior lacerate foramen.

All previous workers (e.g. Cope, 1880a; Scott, 1889; Matthew, 1910; Hough, 1953; Brunet, 1967) have identified the medial-most foramen of this complex as the posterior carotid foramen. It is not. This foramen is the posterior end of a canal deeply grooved into the basioccipital and basisphenoid (see Figure 32), bounded laterally by the petrosal, and floored ventrolaterally by the entotympanic for only a very short extent and then relatively narrowly because of the depth of the channeling into the basioccipital. The channel opens into the braincase at the level of the anterior end of the promontorium but well medial to the petrosal, above the basisphenoid, and clearly medial to the foramen here confluent with the end of the basicapsular fissure--the internal carotid foramen. This canal between the petrosal

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and basioccipital is the petrobasilar canal and, if homologous with the canal in the same position in extant carnivorans, housed the inferior petrosal venous sinus. Confusion has arisen in part because of the unusual condition in nimravids, visible externally, of there being a bony separation formed by an entotympanic/exoccipital contact medial to the posterior lacerate foramen, between the latter and the exit of the inferior petrosal venous sinus, the petrobasilar foramen.

Internal carotid foramen.--Interpretation of the anteromedial portion of the tympanic roof is difficult. It is clear that there is no carotid canal within the entotympanic, nor is there any trace of a groove on the dorsal surface of the entotympanic. However, every specimen that is missing the anterior portion of the entotympanic displays some sort of gap at the anteromedial corner of the petrosal, lateral to the channel for the inferior petrosal sinus. This ranges from a well defined foramen as in Dinictis felina (AMNH 455) to an ill-defined fenestra as in F:AM 62034 and 104823. When the entotympanic is in place, the only route to this foramen consistently available in all specimens examined is across the anterior tip of the promontorium and between the promontorium and the anterolateral corner of the dorsal lip of the entotympanic. There is consistently present a depression in the promontorium in this position, a shallow

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groove aimed at the foramen. When the entotympanic is in place, the opening left is small, but such is predicted by the small size of the genuine, laterally placed posterior carotid foramen.

Other openings are variably present in the fissure of the piriform fenestra. In the specimen with the most complete bulla, the type of Dinictis cyclops (AMNH 6937), the piriform fenestra is the mostly completely closed, with only the intratympanic opening to the internal carotid foramen definitely present, and a possible foramen more medially placed along the sphenoid-petrosal suture, perhaps for the greater superficial petrosal nerve. Both AMNH 455 and F:AM 62034 exhibit irregular fenestrae at the medial end of the tympanic cavity, on the edge of the fossa muscularis major. Their inconsistency, irregularity, and bilateral asymmetry suggests that these are remnants of the piriform fenestra and did not function to conduct major nerves or blood vessels in the adult.

Posterior carotid foramen.--It has been pointed out above that the petrobasilar foramen has been repeatedly misidentified in previous studies as the posterior carotid foramen. In fact, there is no trace of a medially placed posterior carotid foramen or canal. The foramen that may be most reasonably identified as a posterior carotid foramen is placed very far laterally and would clearly have transported a laterally-placed internal carotid or

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perhaps a stapedial branch of the internal carotid artery.

The posterior carotid foramen is preserved on the right side in AMNH 6937, in which it is positioned very far dorsally, just above the ventral edge of the exoccipital. A bony groove across the broken edge of the entotympanic in F:AM 104823 is interpreted here as the dorsal half of the posterior carotid foramen in that specimen.

Other foramina and fenestrae.--Very minute pterygoid foramina, the posterior openings of the pterygoid canal between the pterygoid and basisphenoid bones, are visible in F:AM 62034, AMNH 455, and 6937. The pterygoid groove in each of these specimens is small but very distinct.

A common depression unites the posterior opening of the alisphenoid canal and the foramen ovale so completely that, when matrix-filled, it appears to be a typical simple foramen ovale. Removal of the matrix reveals, in every case examined, the posterior aperture of the alisphenoid canal in the anteromedial wall of this depression. This condition is a little more extreme than that in the Canidae, for example.

One may observe two small foramina in the petrotympanic fissure of AMNH 455, and at least one and possibly two corresponding grooves in the posterior wall of the squamosal (medial to the postglenoid process) on the left side of F:AM 62034. One would presumably be for

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the exit of the chorda tympani nerve from the ear region, and the other perhaps for the corresponding artery, or perhaps for an inferior ramus of the stapedial artery.

A moderately sized postglenoid foramen is present, positioned rather medially: it is dorsal to the medial edge of the postglenoid process. There is variation within Dinictis in the size of this foramen: AMNH 6937 (Dinictis cyclops) shows moderate reduction of the postglenoid foramen, while that of F:AM 62034 is fairly large, and that of AMNH 455 (Dinictis felina) is intermediate in size.

The stylomastoid foramen has been described above, in the discussion of its defining elements. It may be noted here that the channeling that Brunet (1967) described in the medial side of the mastoid is of variable depth in the specimens examined here, ranging from shallow grooves to more distinct grooves, but never is the groove as deep as the full radius of the implied tube.

Two puzzling structures are found on the posterolateral margin of the auditory region. In some specimens (e.g. F:AM 62034, AMNH SD 230-4152, and 104823), a small cavity occurs in the occipital and mastoid walls at the suture between the two. This cavity is irregular and rough-walled and presents the appearance of having failed to ossify. The entotympanic covers this area smoothly with no sign of a bulge into this space, so it

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does not represent an invasion of the occipital and mastoid by the hypotympanic sinus. In other specimens (e.g. AMNH 455 and 6937), there is no rough-walled cavity but there is a distinct emargination of the occipital just medial to the suture with the mastoid. The groove defining this emargination is dorsally confluent with the posterior lacerate foramen between the petrosal and occipital.

Traces of the path of the auricular branch of the vagus nerve remain in several cases. A small foramen between the mastoid and entotympanic, just posteromedial to the stylomastoid foramen, is present in AMNH 6937. Absence of the entotympanic in AMNH 455 reveals a small canal in a comparable location between the caudal tympanic process of the petrosal and the mastoid, exiting from the posterior wall of the facial canal. The caudal tympanic process of the petrosal is partially broken in the right auditory region of F:AM 62034, leaving the dorsal half of the canal. Posteriorly a groove runs towards the posterior lacerate foramen.

Adjacent Cranial Morphology

Basisphenoid.--A distinct pterygoid groove is present, running from within the osseous auditory tube anteromedially to the small opening of the pterygoid canal. At the anteromedial corner of the auditory region,

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the basisphenoid forms a buttress up against the curve of the entotympanic. The size of this prominence varies within Dinictis: D. felina (AMNH 455) displays a relatively large one, while that of F:AM 62034 is less pronounced. Although the resulting overall shape of the anteromedial corner of the auditory region is very much the same as that found in other carnivorans, it is to be contrasted with a common carnivoran condition in which this shape results from the projection anteriorly of a sharp anteromedial process of the auditory bulla. Thus the basisphenoid of other carnivorans may present a low, ventrally directed ridge along the medial side of the bulla, but it rarely cups around the anterior margin of the bulla because of the presence of a anteromedial process, and therefore does not usually form the buttress observed in Dinictis.

Basioccipital.--The edges of the basioccipital are produced into a sharp flange, directed ventrally from the rugose area against which the entotympanic is appressed. This area of contact with the entotympanic is rather flat and nearly vertical. Dorsally, the basioccipital is channeled for the petrobasilar canal. The posterior third of this canal is roofed by a basioccipital projection that abuts the posteromedial corner of the petrosal. Angling immediately dorsomedially, the canal passes between the petrosal and basioccipital to the dorsal surface of the

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basioccipital. A sharp ventral margin to this canal extends the length of the auditory region, but is not anywhere produced into a particularly wide flange.

Lateral margin of auditory region.--As mentioned earlier, the glenoid fossa is slightly pedestalled, a morphological feature correlated with the degree of sabertoothy. The postglenoid process is large, and directed almost straight ventrally rather than ventromedially. A moderately deep tympanic notch results from the pedestalling and the length of the postglenoid process, and is roofed by a lateral shelf of squamosal.

A moderately large mastoid process forms the posterior wall of the tympanic notch. Again, the well developed mastoid process is a feature correlated with sabertoothy. The ventral tip of the mastoid process is rugose, and often squared off and flattened, for muscle attachment.

The processus hyoideus projects medially from the medial wall of the mastoid process, forming the anterior wall of the facial canal, and extending around in AMNH 6937, the most complete specimen, to the caudal process of the petrosal and ventrally to the entotympanic. A groove in the posterior surface of the ectotympanic, ventral to the hyoid process and anterior to the stylomastoid foramen, suggests that the hyoid apparatus articulated just anterior to the distal third of the facial canal,

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immediately posterior to the ectotympanic.

In F:AM 62034 and AMNH 455, there is a groove or fissure on the anteromedial side of the dorsal half of the mastoid process; this fissure is continuous with the squamosal-petrosal suture in the roof of the tympanic cavity and may represent the suture between the squamosal and mastoid. The squamosal forms a small flange on the anterior face of the hyoid process, but the hyoid process proper extends out well beyond the squamosal; there is no evidence that the articulation of the hyoid process would involve the small squamosal flange.

A broad expanse of bone connects the mastoid process and the large, leaf-like, posteriorly directed paroccipital process. This region is larger and rather more independent from the bulla than is typical for most other carnivorans.

Intracranial Morphology

The matrix has been removed from the cranial cavity of AMNH SD 230-4152, so that the dorsal surfaces of both petrosals are available for examination, as well as some of the surrounding intracranial structures on the left side. All of the following description is of this specimen unless otherwise stated.

Petrosal.--In intracranial aspect, the general outline of the petrosal is squarish or rounded: the

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rostral apex is blunt and the dorsal (mastoid) extension in the posterolateral corner of the braincase is short and broad. A well defined crista petrosa is lacking, there being present instead only a rounded ridge. Part of the small surface anterior to the petrosal crest is occupied by a shallow sulcus that runs parallel to and adjacent to the crest (see Figure 33). This anterior face is little covered by the squamosal, if at all, because of the lack of development ventrally of the tentorium.

The dorsomedial intracranial face of the petrosal is relatively large, with a pronounced ridge-like prominence from the anterior margin of the internal auditory meatus to the anterior edge of the petrosal. A slight ridge above a pit on the posterior portion of the petrosal appears to continue the line of the anterior ridge. Part of the pars mastoidea that forms the posterolateral corner of the braincase extends from the edge of the petrosal in a short, broad process, across which runs the sulcus for the sigmoid sinus.

Two major features interrupt this cerebellar face of the petrosal: the internal auditory meatus and the subarcuate fossa. The internal auditory meatus in Dinictis is large and an indented ovoid in shape. As in felids, the transverse crest is deep within the meatus, and anterior to the meatus. No finer divisions can be seen within either the anterodorsal foramen or the

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posteroventral foramen formed by the crest. Dorsal to the internal auditory meatus lies a shallow subarcuate fossa, slightly deeper and better defined on the left side than on the right.

The path of the trigeminal nerve across the anteromedial part of the petrosal is marked only by the sulcus ventromedial to the ridge from the anterior margin of the internal auditory meatus: the lack of a pronounced petrosal crest precludes the presence of a trigeminal canal as seen in the dog or raccoon. Immediately lateral to this sulcus, on the anterior margin of the petrosal, a foramen opens into a groove leading into the small piriform fenestra. This foramen and groove are identified as the hiatus Fallopii and proximal part of the Vidian groove respectively.

Just anterior to the posterior edge of the petrosal, on a level between that of the subarcuate fossa and that of the internal auditory meatus, a cleft forms an elongate foramen that may be identified as the posterior end of the canal for the vestibular aqueduct. A couple of millimeters ventromedial to this foramen is another, very distinct, small oval foramen, right on the posterior margin of the petrosal. On both sides of AMNH SD 230-4152, the posteroventral corner of the cerebellar face of the petrosal is imperfectly preserved. However, on both sides but especially on the right side, a few

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millimeters anterior to the edge of the posteromedial corner, part of a slit-like foramen may be identified. In extant carnivorans, this is the posterior opening of the cochlear aqueduct. A typical notch (as is usually found in canids or ursids) in the emargination of the petrosal at the posterior lacerate foramen may be seen in ventral view in F:AM 62034, marking the position of the opening of the cochlear aqueduct.

Intracranial channels.--The presence of a channel for a superior petrosal sinus may be inferred from the presence of a moderately sized postglenoid foramen for the external jugular vein, although it is not visible intracranially. A medial extension of squamosal abuts the entire length of the anterodorsal margin of the petrosal, completely enclosing the ventral portion of the transverse sinus canal and all of the superior petrosal sinus canal.

Posteriorly, a large channel for the sigmoid sinus is well defined, curving across the posterodorsal margin of the petrosal, across the dorsal process of the pars mastoidea (see Figure 33), and down behind the petrosal to the rather laterally placed posterior lacerate foramen. From the posterior-most point of the sigmoid sinus channel, just dorsal to the exit of the channel into the posterior lacerate foramen, a foramen leads into a condyloid canal, which ends in a foramen on the lateral wall of the foramen magnum.

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At the bend in the sigmoid sulcus in AMNH SD 230-4152 (at the posterodorsal corner) there is a failure to ossify that may be a foramen through the occipital corresponding to the channel to the mastoid foramen in Hoplophoneus. The external opening in this specimen of Dinictis is slit-like rather than rounded. No such foramina can be identified on F:AM 62034 or USNM 15889. F:AM 104823 has a pair of very small foramina, one of which is slit-like, in the position of the mastoid foramina in Hoplophoneus. Dinictis cyclops (AMNH 6937) also has a pair of well defined foramina very slightly more ventrally placed but comparable to those in F:AM 104823 and Hoplophoneus.

All Dinictis specimens well enough preserved to determine the morphology in the appropriate region have large post-parietal foramina, rather more ventrally placed than in Hoplophoneus relative to the main swelling of the braincase. Although no specimen is dissected at the appropriate level to demonstrate this, the post-parietal foramen is inferred from its position to have opened into the channel for the transverse sinus intracranially.

Unlike most carnivorans, the medial margin of the petrosal in Dinictis is neither relatively straight, nor is it channeled for the inferior petrosal sinus. Rather, there is a medial-most point at the level of the most prominent part of the promontorium, and the edges angle laterally away from that point both anteriorly and

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posteriorly. The channel for the inferior petrosal sinus is excavated in the basioccipital, floored by only a narrow crest of basioccipital (and completely floored, of course, by the entotympanic) but roofed posteriorly by a broad shelf of basioccipital. Anteriorly, the petrobasilar fissure is large and open, floored by the entotympanic.

On both sides of AMNH SD 230-4152, a small channel from the posterior margin of the foramen ovale to the meningeal grooves is distinctly visible. In many extant carnivorans, this channel carries an anastomotic ramus from the internal maxillary branch of the external carotid artery through the foramen ovale to the medial meningeal artery.

NIMRAVUS

Based in detail on AMNH 6930 (r), AMNH 6931 (l), F:AM 62020 (l & r), F:AM 99259 (l; juvenile), and YPM 14385 (r).

Tympanic Floor: Auditory Bulla

Ectotympanic.--Only three specimens have enough of the ectotympanic preserved to demonstrate relevant details of its structure--AMNH 6930, F:AM 62020 and 99259. This

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gently curved plate of bone forms the anterolateral and anterior margin of the bulla, extending from the anteromedial corner of the mastoid process tc the anteromedial corner of the auditory cavity. The anterior crus of the ectotympanic has a particularly elongate horizontal arm, nearly closing the oval of the tympanic ring by extending to within two or three millimeters of the dorsal tip of the posterior crus. Even the juvenile skull (F:AM 99259) exhibits a tympanic ring lying in the vertical plane. The ring is oriented in this specimen as well as in the adults, AMNH 6930 and F:AM 62020, at nearly 45 degrees from the sagittal plane. A well defined tympanic sulcus lies next to a low crista tympanica. The line of the latter forms a large oval, and extends not only onto the crura of the ectotympanic but is apparently continued by a low ridge on the portion of the squamosal roofing the gap between the crura (F:AM 62020 and YPM 14385).

A greater thickness of the ectotympanic anteriorly results in the plane defined by the bony edge of the external auditory meatus projecting roughly 30 degrees from the sagittal plane, i.e. more anteroposteriorly than is the plane of the tympanic membrane itself. No osseous external auditory meatal tube is present. Instead, the osseous meatus is a large ovoid, wider than the tympanic notch in the squamosal, although not quite as large as the

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oval of the crista tympanica. As in Dinictis, the relatively large size of the meatus in combination with its orientation causes the anterior part of the meatus to be placed quite far rostrally so that it lies directly medial to the postglenoid process. In adults, the result is that the auditory cavity extends more anteriorly than is typical for carnivorans; this is even more exaggerated in the skull of the juvenile, F:AM 99259, in which the external auditory meatus appears to face directly into the postglenoid process.

Neither the anterior nor posterior crus of the ectotympanic fuses with the squamosal. YPM 14385 exhibits an irregular shallow concavity in the squamosal to receive the anterior crus, immediately posteromedial to the postglenoid foramen. The entire anterior crus is rather broadened and flattened, with a blunt end. Posteromedially, the anterior crus sends off a long thin process, the processus tubarius, which can be seen in F:AM 62020 and 99259 to end in a small knob, in this taxon dividing the epitympanic recess from the deep anterior recess in the sphenoid and squamosal. (This latter recess is described below; also see Figure 34.) F:AM 62020 and 99259 clearly demonstrate that this medial process from the anterior crus extends as far medially as any part of the incus or malleus (both of which appear to be approximately in place in the left auditory cavities of

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these two specimens).

The posterior crus is directed entirely dorsally, resting in a shallow concavity on the anteromedial corner of the mastoid process just lateral to the hyoid process of the mastoid.

Apparently complete posterior halves of the ectotympanics in F:AM 99259, 62020, and AMNH 6930 show a smooth curve of the ventral margin towards the posterior crus. A broadened, flattened or sulcate ventral edge appears to be an unbroken, natural edge of the ectotympanic and looks very much like a surface of articulation with a cartilaginous entotympanic. This surface is flat ventrally but channeled in the center along the posterior-most extent of the ectotympanic margin.

Although the tympanic ring is complete in AMNH 6930, F:AM 62020, and F:AM 99259, the ventral part of the ectotympanic flange appears broken anteriorly, so the extent of expansion of the ectotympanic anteroventrally is not known. That part of the ventral extension, beyond the annulus proper, that is preserved is generally rather flat, and only gently concave internally, so that the crista tympanica and tympanic sulcus are only slightly produced into the tympanic cavity. There is certainly no particular expansion of the hypotympanic sinus below the meatus.

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F:AM 62020 (Figure 35) does exhibit an extension of the ectotympanic ossification anteromedially that appears to be a well ossified canalis musculotubarius for the auditory tube and tendon of the tensor veli palatini. In this specimen, the broken part of the ventral edge appears to extend only as far anteriorly as the intrabullar end of the osseous auditory tube; the rest of the anterior margin is smooth and rounded, suggesting that the ventral flange of the ectotympanic did not extend any farther forward, and that the anterior edge was emarginate as in Dinictis. Anteriorly, the osseous canalis musculotubarius extends to the level of the foramen ovale, and medially to the basisphenoid. Along its posteromedial margin, a canal runs between this osseous canalis musculotubarius and the anterior edge of the entotympanic, from the anteriomedial-most corner of the bulla posterodorsally along the epitympanic wing of the sphenoid to the internal carotid foramen. (See Figure 34.) The ectotympanic is emarginate on the posterior (intrabullar) surface of the osseous canalis musculotubarius, between the crista tympanica and the internal opening (posterior end) of the auditory tube, allowing a slight anteromedial extension of the tympanic cavity (see Figure 35), in the direction of and underlying the anterior auditory sinus.

Not enough of the ventral portion of the bulla is preserved to indicate whether a styliform process was

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present or not. The crest on the ventral surface of the elongate osseous canalis musculotubarius may have served as the site of origin of the levator veli palatini muscle. This crest even appears broken as if it were the base of a process, in which case such a projection might have been functionally a styliform process.

Accessory ossification.--Several specimens of Nimravus (AMNH 6930, 6931, F:AM 62020, and 99259) exhibit an accessory ossification in the angle between the ectotympanic and the postglenoid process. This ossification is shown in position in Figure 35, and in isolation in Figure 37. In overall shape, the bone is rather seed-like, but with a smooth concave dorsal surface that forms a ventral part of the external auditory canal. The bone's rounded ventral surface is pitted and rugose, as if it were embedded in cartilage in life. When the ossification is in position, a smooth anterolateral surface continues the posterior wall of the postglenoid foramen ventrally, so that the original postglenoid foramen is not visible externally and a secondary postglenoid foramen is visible ventral to the original foramen, between this ossification and the postglenoid process. This positioning of the ossification means that it forms a bony separation between the fairly large postglenoid foramen (presumably conducting the external jugular vein) and the auditory canal.

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There is no evidence of any fusion between this ossification and any of the surrounding bones. This accessory bone barely touches the squamosal on each side of the channel from the primitive postglenoid foramen, and abuts the ectotympanic along a single line. That this element is a separate ossification center and not merely a bony outgrowth of any of the usual elements is further supported by the presence of a thin layer of matrix between the tiny element and the ectotympanic and even more matrix between the ossification and the squamosal in the juvenile skull, F:AM 99259. This lack of fusion or even any complex articulation is doubtless the reason for the failure to preserve this element in place in the majority of Nimravus specimens. That good preservation generally of the ear region is related to this element's preservation is indicated by the observation that the two specimens with ear ossicles (malleus and incus) intact are two of the four specimens with the extra ossification preserved.

Entotympanic.--In no specimen is a complete entotympanic present. If the inference from the finished edge on the ectotympanic is correct that a cartilaginous floor was present, then one would not expect an enclosed, fully ossified bulla. However, clear faceting on the occipital bones, the posterior edge of the petrosal, and along the caudal process of the petrosal to the facial

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canal, indicates that the ossified sheet of entotympanic might be expected to continue around the ear region to the stylomastoid foramen. In fact, the only portion of entotympanic ever preserved in the available specimens has been the medial wall, lying appressed or parallel to the basioccipital and basisphenoid (AMNH 6930, F:AM 62020 and 99259).

The entotympanic in adult Nimravus is composed of two layers of very thin bone (easily damaged in preparation). Both layers are clearly visible at the edges of the fragments of entotympanic in F:AM 62020 and AMNH 6930. In the juvenile skull, F:AM 99259, double layers are not apparent in the larger pieces of entotympanic present. On the left side, the fragment is small and crushed, but on the right side, there is a larger piece in natural position, which appears from the edge to be solid and very thick rather than bilaminar. It may be, however, that the piece of entotympanic present on the right side represents the complete extent of ossification at that stage, and that the apparently solid edge is the natural margin. A small cross-section of the crushed fragment on the left side does show that the entotympanic near its petrosal edge is bilaminar with a matrix-filled space between the layers.

In F:AM 62020, the dorsolateral part of the anterior edge of the entotympanic is intact. This margin closely

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parallels the underlying basisphenoid (rather than descending more vertically into the margin of a partial 'septum' as in Dinictis, AMNH 6937). The more ventral part of this anterior margin is incomplete, so a very reduced partial septum is not precluded, but neither is there any direct evidence for such a feature. Indeed, the anterior extension of the ectotympanic is low, without the ventral extension seen in Dinictis and with no facet or wall against which an incurved entotympanic septum might abut. I conclude, therefore, that Nimravus very probably did not have even the short partial 'septum' seen in Dinictis.

No groove or canal for a medially situated internal carotid artery has been seen. The foramen that has been previously identified as the posterior carotid foramen (e.g. Cope, 1880a; Hough, 1953; Brunet, 1967) is shown here to be the petrobasilar foramen--the posterior opening of the petrobasilar canal for the inferior petrosal sinus. There is certainly no sign of a canal or channel within the entotympanic as is typical for other carnivorans.

None of the Nimravus specimens available for this study had the posterior wall of entotympanic complete, so the presence of a foramen for a more laterally situated internal carotid artery cannot be determined.

Tympanic Roof

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The auditory region in Nimravus is deeply excavated and slightly laterally compressed. The promontorium faces slightly anterolateraly as well as ventrally. Lateral and anterior to the promontorium, the tympanic cavity is deeply excavated into the tympanic roof. On the medial side of the auditory region, the production of the edge of the basisphenoid and basioccipital into a sharp, ventrally directed flange, and on the lateral side, the slight pedestalling of the glenoid fossa for the mandibular articulation, both further accentuate the depth of the auditory region.

Petrosal.--The promontorium is low and smoothly rounded. Medially, a long straight contact with the basioccipital (the flange dorsal to the petrobasilar canal) is visible in YPM 14385. A secondary contact or near contact with the ventral basiocipital flange below the petrobasilar canal occurs in some specimens (e.g. F:AM 62020 and AMNH 6931), just at the middle of the medial margin of the promontorium. At the posterior corner of the petrosal, a lateral projection from the basioccipital borders part of the posterior margin of the petrosal. Lateral to the posterior lacerate foramen, the petrosal has a moderately broad contact with the exoccipital.

A small anterior corner of the petrosal is underlain by the entotympanic anteriorly. In the left ear of F:AM 62020, the entotympanic abuts the medial edge of the

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petrosal without the overlap seen in the other nimravids. The posterior skirt of the promontorium shows a clear facet where the petrosal and entotympanic again overlap. (That the facet reflects this overlap is confirmed by a fragment of entotympanic in place on this ledge in the right auditory regions of both AMNH 6930 and F:AM 62020.)

The aperture of the cochlear fossula is directed posteroventrally and slightly laterally in Nimravus. The horizontal channel into the fossula ranges from very shallow (AMNH 6930 and F:AM 62020) to deep (YPM 14385 and F:AM 99259) and even cleft-like (AMNH 6931).

Posteromedially from the cochlear fossula, just beside the edge of the facet for the entotympanic, there is a small anterolaterally directed foramen in the promontorium. This unidentified foramen is questionably present in YPM 14385, clearly present on both sides in F:AM 62020, and in the left ear region of F:AM 99259. No such foramen can be seen in AMNH 6931, but in the left auditory region of that specimen, the petrosal margin of the posterior lacerate foramen appears to be notched, a feature not observed in any other Nimravus to date. In the right auditory region of AMNH 6930, there is such a foramen present but instead of being positioned anterior to the entotympanic, it appears to be covered by the entotympanic or to open just posterior to the contact between the entotympanic and petrosal, immediately

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anterior to the posterior lacerate foramen.

The caudal process of the petrosal forms a bridge beneath a canal for the auricular ramus of the vagus nerve in the best preserved specimen, F:AM 62020. In the juvenile, F:AM 99259, the caudal process of the tympanic contacts the mastoid more anteriorly, forming an enclosed facial canal for a short distance; the path of the auricular branch of the vagus is not clear but there appears to be a short canal entirely enclosed by mastoid.

Most promontoria have poorly preserved ventral surfaces. Those in F:AM 99259 are undamaged, however: on both sides there is a very faint, anteroposteriorly oriented, shallow groove across the lateral side of the promontorium. Several much more distinct grooves are visible on the promontoria in both sides of the basicranium of F:AM 62020. These grooves run from just medial to the opening of the cochlear fossula, forward, curving medially to end at the anteromedial-most point of the portion of the petrosal not covered by entotympanic. In none of these skulls is there any groove aimed at the vestibular fenestra or running between the aperture of the cochlear fossula and the vestibular fenestra, and thus no evidence from grooves for a stapedial artery.

In Nimravus, the moderately sized, oval vestibular fenestra is deep within the auditory region, directed anterolaterally. As in Dinictis, there is variation in

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the position of the facial foramen. It is immediately dorsal to the vestibular fenestra in F:AM 62020, while in YPM 14385, the channel of the facial canal extends along the anterior margin of the promontorium, and the facial foramen itself is quite medially placed.

From the point dorsal to the vestibular fenestra, the facial sulcus runs ventrally and posterolaterally between the promontorium and the mastoid, and sharply ventrally behind the hyoid process. In F:AM 62020 and perhaps in F:AM 99259, there is an additional flange from the posterior side of the hyoid process forming an anteromedial wall to the facial canal. The caudal process of the petrosal on each side is very similar to that of the other side in F:AM 62020, and therefore appears complete. However, in this specimen, the process is not involved in the walls of the facial sulcus, stopping well short of it. In contrast, the caudal process of the petrosal in F:AM 99259 is co-ossified with the hyoid process and the mastoid, forming a completely enclosed facial canal.

The epitympanic recess is a well defined circular concavity in YPM 14385--less clearly seen in the more complete specimens with ectotympanic and ear ossicles in place. In the former, the suture between the squamosal and petrosal is visible, running through the center of the recess. As in Dinictis, there is a deeper pit in the

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petrosal half of the epitympanic recess to accomodate the posterior crus of the incus. Preservation is not good enough in YPM 14385 to permit with any certainty the discernment of foramina in or near the epitympanic recess.

Medial to the epitympanic recess is the fossa muscularis major, a well defined and moderately deep oval recess for the origin of the tensor tympani muscle. The anterior margin of this recess, the anterior edge of the epitympanic wing of the petrosal, lies against the sphenoid and squamosal epitympanic wings, completely closing the piriform fenestra except for a small gap at the center of the anterior petrosal margin, just lateral to the edge of the entotympanic (F:AM 99259) and at the end of the grooves across the promontorium (F:AM 62020) (see Figure 35).

Sphenoid.--Epitympanic wings from the alisphenoid and perhaps basisphenoid completely roof the anterior part of the tympanic cavity. The edge of the facet on the basisphenoid for the medial entotympanic is well marked by a smooth channel, presumably for an anastomotic branch from the ascending pharyngeal artery (YPM 14385; see Figure 34). Part of this channel is clearly visible in the left ear of F:AM 99259 and the right ear of F:AM 62020; the rest of the canal is filled in the latter with matrix in a cast of the canal.

Medial to this channel is a ridge of bone marking the

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anterior margin of the adjacent entotympanic, and anterior to it a broad channel, which presumably overlay the cartilage of the auditory tube. In F:AM 62020, this channel forms the roof of the osseous canalis musculotubarius, floored by the trough of ectotympanic. Within this channel lies the pterygoid groove.

In the center of the anterior wall of the tympanic cavity, Nimravus has a large oval pocket or excavation into the sphenoid (Figure 34). This excavation varies somewhat in its depth; the wall extending ventrally from a shallower (but well defined) pocket slopes very slightly anteriorly in F:AM 62020, while the deeper pocket in YPM 14385 results in a rounded, posteriorly directed shelf below the pocket and a more vertical wall down from the pocket before the anterior margin of the auditory region is reached. In the juvenile, F:AM 99259, the ectotympanic partly obscures this area, but the excavation appears shallower than that seen in the adults.

This excavation (here dubbed the 'anterior auditory recess') is directly anterior to (and much larger than) the fossa muscularis major; the two recesses are separated by a ridge composed of the edges of the sphenoid and the petrosal. Posterolaterally, the large anterior auditory recess is separated from the epitympanic recess by a ridge of bone at the edge of the squamosal and by the long posteromedial projection, the processus tubarius, from the

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anterior crus of the ectotympanic.

Squamosal.--Lateral to the sphenoids, the squamosal forms the slightly pedestalled glenoid fossa and postglenoid process. A low ridge or long prominence of bone runs from the top of the tympanic notch to the end of the postglenoid process, just lateral to the postglenoid foramen. The squamosal gently slopes away anteriorly on each side of this prominence, so the lateral half of the wall of the postglenoid process faces slightly laterally as well as posteriorly, while the medial half (containing the postglenoid foramen) faces posteromedially. The squamosal shelf above the tympanic notch is only of moderate width, and the expanse of squamosal lateral to the postglenoid foramen is not great.

A channel extends ventrally from the postglenoid foramen. The pronounced walls of this channel abut the accessory ossification described above. Dorsal to the foramen, a shallow pocket and rugose area in YPM 14385 marks the articulation with the anterior crus of the ectotympanic. Just medial to the postglenoid foramen and process, a distinct groove or pair of grooves (presumably for the chorda tympani nerve and associated artery) can be seen in the right ear region of YPM 14385, and in both sides of F:AM 62020, running from the tympanic cavity down and medial to the glenoid fossa.

Auditory ossicles.--Two specimens, F:AM 62020 and

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99259, retain the incus and malleus roughly in place in the left auditory regions (and in the latter specimen, in the right side as well). In neither specimen has preparation been carried so far as to remove the ossicles, because of their fragility and the present scarcity of comparative material. It can be seen at this stage, however, that the neck on the malleus is extremely long, perhaps related to the depth of the tympanic cavity. The posterior process is short, small, and simply pointed (see Figure 36). The manubrium is long and slender.

Principal Tympanic Spaces and Foramina

In spite of the lack of invasion of the mastoid or occipital by the hypotympanic sinus, the total volume that would have been enclosed by a regularly shaped bulla, with walls of the shape indicated by the fragments preserved in these specimens, would have been fairly large. The basioccipital flange is large and cup-like, arguing for an inflated, rather globular entotympanic. A large facet on the medial side of the mastoid also indicates a large bulla; the ventral edge of the facet is placed more laterally in Nimravus than in Dinictis, so that although the mastoid and paroccipital processes are still broadly connected, the bulla may be inferred to have been more laterally inflated. Furthermore, the depth of the auditory region would result in a fairly large

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hypotympanic space even if the entotympanic was not much inflated beyond the ventral edge of the ectotympanic and basioccipital flanges.

Tympanic cavity.--The tympanic cavity proper is narrow and deep--an elongate slot between the ectotympanic (and squamosal) and the anterolateral side of the promontorium. The anterior auditory recess, described above, extends the tympanic cavity dorsal to the ectotympanic and anteriorly into the sphenoid.

Epitympanic recess.--A small, shallow, circular concavity, the epitympanic recess lies on the suture between the squamosal and petrosal. In the petrosal portion of the recess, a deeper pocket is excavated, presumably for the posterior crus of the incus and the suspensory ligament.

Posterior lacerate foramen and adjacent foramina.--The posterior lacerate foramen is rather laterally positioned, in the center of the posterior margin of the auditory region. Posteromedially, a high wall of bone separates the posterior lacerate foramen from the hypoglossal foramen. Medially, a bony bridge between the occipital and the entotympanic completely separates the posterior lacerate from the petrobasilar foramen. The posterior lacerate foramen varies in shape from a simple large circle (YPM 14385) to a distinctly 'double-barrelled' shape (F:AM 62020), as if two large

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vessels exited side-by-side.

Cope (1880a), Hough (1953), and indeed all others publishing discussions of the ear region of Nimravus to date have misidentified the medial-most foramen in this region as the posterior carotid foramen. Examination of well prepared specimens (e.g. YPM 14385 and F:AM 62020) now demonstrates that this foramen is more likely the posterior end of the petrobasilar canal for the inferior petrosal venous sinus. This foramen normally opens into the wall of the posterior lacerate foramen intracranially, but here is separated from the posterior lacerate foramen by a bony bridge between the occipital and entotympanic. Compared with the posterior lacerate foramen, the petrobasilar foramen opens more dorsally, near the hypoglossal foramen, and may be said to be confluent with the latter in some specimens (e.g. F:AM 62020).

Internal carotid foramen.--In the two best preserved specimens, YPM 14385 and F:AM 62020, there is a distinct gap at the corner where entotympanic, promontorium, and sphenoid all meet. The grooves across the promontorium in F:AM 62020 run into this fenestra. In YPM 14385, the entotympanic is entirely missing, and the gap can be seen to extend medially to a foramen (mostly defined by a small emargination in the edge of the sphenoid) positioned at the dorsal end of the canal (perhaps for an anastomosus from the ascending pharyngeal artery) in the epitympanic

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wing of the sphenoid. This medial foramen is here considered homologous with the internal carotid foramina of other taxa, on the basis of its position.

Posterior carotid foramen.--None of the specimens of Nimravus that I have examined have any foramen, either medially or laterally placed, that I would regard as a posterior carotid foramen. It is not safe to conclude from this that one was not present, however; in no specimen examined is the posterior wall of the entotympanic complete enough to show whether any foramen comparable to those of Dinictis, Hoplophoneus, or Barbourofelis was present.

Other foramina and fenestrae.--Small pterygoid grooves lead in Nimravus to pterygoid foramina, positioned in F:AM 62020 and YPM 14385 unusually ventrally, on the medial walls of the pterygoid processes. In the juvenile, F:AM 99259, the pterygoid canal is well preserved on the right side: it is relatively larger than in adults, and its posterior opening more typically positioned on the dorsal roof of the nasopharyngeal chamber, at the base of the pterygoid processes.

A common, oval depression encloses the posterior aperture of the alisphenoid canal (facing posterolaterally) and the foramen ovale (facing ventrally).

In the left auditory region of F:AM 62020, the

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preservation of the ectotympanic permits discernment of two small, slitlike foramina in the petrotympanic fissure, for the vessels filling the grooves on the posterior wall of the squamosal.

The postglenoid foramen proper is large in all Nimravus examined thus far, but is not actually visible when the accessory auditory ossification is preserved in its correct position. Instead, a secondary postglenoid foramen is formed between this ossification and the canal in the squamosal ventral to the postglenoid foramen proper.

A completely enclosed facial canal is present in F:AM 99259, formed by the hyoid process of the mastoid anteriorly, a channel in the medial wall of the mastoid process laterally, and a long caudal process of the petrosal medially and posteriorly. This enclosed canal is in sharp contrast to the open sulcus in F:AM 62020, bounded entirely by the hyoid process and mastoid proper and without any involvement of the caudal process of the petrosal. YPM 14385 is lacking even a well defined sulcus, having only a shallow channel on the medial face of the mastoid, but this could be due in large measure to breakage of the delicate flanges in this extensively fractured specimen. Lack of preserved entotympanic in this area prevents deciphering of the contribution from the entotympanic to the definitive stylomastoid foramen.

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Two of the John Day specimens, AMNH 6930 and YPM 14385, exhibit a gap in the anterior-most section of the occipital-mastoid suture. This irregular cavity looks very much like a failure to ossify completely. In contrast, F:AM 62020 shows nothing comparable, but, immediately lateral to the suture, exhibits a distinct groove descending from the junction between the mastoid and the caudal process of the tympanic ventrally to the edge of the auditory cavity.

F:AM 62020 shows on both sides a clear canal for the auricular branch of the vagus nerve dorsal to the caudal process of the petrosal. Immediately lateral to the posterior opening of this canal is the base of the unidentified groove or grooves in the mastoid. And medial to this area, in several specimens, is the unidentified foramen in the promontorium (see the earlier section on the petrosal on p. 251).

Adjacent Cranial Morphology

Basisphenoid.--No suture is distinguishable between the alisphenoid and basisphenoid, so the degree of contribution of the basisphenoid to what is called here the epitympanic wing of the sphencid is unclear. Medial to the tympanic region, the basisphenoid contributes to the medial ventrally-directed flange against which the entotympanic is appressed. These flanges are relatively

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small in the juvenile, but fairly well developed in the adults. At the anterior-most corner, the flange curves around so that a sort of buttress is formed. The overall shape of this region is very much like that found in many other carnivorans, often produced in other taxa by an anteromedial process of the entotympanic lying on the basisphenoid rather than solely by the basisphenoid itself.

Basioccipital.--In F:AM 99259, the suture between the basisphenoid and basioccipital can be seen towards the level of the anterior end of the auditory region. The lateral margins of the basioccipital project ventrally in large, sharp flanges which cup the bulla. These flanges are longer and more pronounced in adult Nimravus than in Dinictis, a taxon otherwise often considered "more derived".

Dorsally, the petrobasilar canal channels deeply into the basioccipital. In YPM 14385, thorough preparation and the lack of any entotympanic reveals a complete dorsal roof to the petrobasilar canal, from the posterior foramen to the level anteriorly where it passes intracranially. The ventral edge of the channel is more variable. In YPM 14385, it is not much extended, so that the petrobasilar canal is between the petrosal and the basioccipital but would have been floored by the entotympanic. The other extreme may be seen in AMNH 6931 or F:AM 62020, in which

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the ventral edge of the canal projects laterally and contacts, or almost contacts, the petrosal.

Some interesting ontogenetic changes are implied by the condition of the median wall in the juvenile, F:AM 99259. The ventral flange of the basioccipital is not as pronounced as in the adults, and the promontorium not as recessed above the level of the basioccipital. Related to this, the medial surface of the basioccipital (against which the entotympanic lies) is more horizontal, facing more ventrally, and the petrobasilar canal smaller.

Lateral margin of auditory region.--The glenoid fossa is very slightly pedestalled, with a moderately sized, ventrally directed postglenoid process. The tympanic notch is fairly open, and proportionately not as deep as in the more sabertoothed nimravids. On the posterior side of the tympanic notch, the mastoid process is square and rugose for muscle attachment, but not long.

As described above, the hyoid process projects medially from the base of the mastoid process, forming the anterior wall of the facial canal. In YPM 14385, a groove through the base of the hyoid process is the ventral extension of the squamosal-petrosal suture after the latter traverses the roof of the tympanic cavity. If this identification is correct, the anterior one-third of the mastoid process is formed by part of the squamosal bone. There appears to have been only a low ridge of squamosal

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on the anterior edge of the base of the hyoid process; the bulk of the hyoid process would have been formed from the medial face of the mastoid process.

The paroccipital process is broad and flattened at its base, long and narrow towards the tip, and directed almost straight posteriorly. This process is larger and more independent of the bulla than is typical for the other Carnivora examined. A crest connects the lateral margin of the paroccipital process with the mastoid process, so that a shelf lateral to the bulla is formed.

Intracranial Morphology

No specimen definitely referable to Nimravus and showing the intracranial surface of the basicranium was available for study.

HOPLOPHONEUS

Based in detail on AMNH 1406 (l & r), AMNH 38981 (l), F:AM 62022 (l), F:AM 62078 (l & internal), F:AM 69417 (l), AMNH 82440 (l & internal), and F:AM 102387 (l).

Tympanic Floor: Auditory Bulla

Ectotympanic.--AMNH 1406, F:AM 69417, and 102387 retain one or both ectotympanics in place; AMNH 82440 has

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the anterior and dorsal portions in place and a broken part of the ventral ectotympanic present but displaced. The anterior crus is broad and elongate, arching over the external auditory meatus. A gap of several millimeters separates the horizontal anterior crus from the tip of the short, vertical posterior crus.

The plane defined by the edge of the crista tympanica is nearly vertical, and at an angle of approximately 60 degrees from the sagittal plane. This is much more transversely placed than in Dinictis or even Nimravus, with the result that (as Hough, 1953: 99 correctly observed) the meatus faces as much forward as laterally, into the posterior wall of the postglenoid process. Because the width of the crista tympanica is greater anteriorly and ventrally, the plane formed by the bony edge of the external auditory meatus is less vertical and less transversely placed, being only about 45 degrees from sagittal. A very low portion of the crista tympanica extends diagonally across the anterior crus, to its posterolateral corner.

No osseous external auditory meatal tube is present. The oval external auditory meatus is slightly wider than the auditory notch, but because of the angle at which it is placed, the meatus extends only slightly past the posterior surface of the postglenoid process.

The broadened anterior crus may be partially fused to

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the squamosal: most specimens retain this fragment of ectotympanic in place. A few other specimens in the American Museum collections with this area free from matrix are lacking the ectotympanic entirely; none of these specimens show any concavity near the postglenoid foramen that might receive the anterior crus, but F:AM 62022 has a well defined, circular depression that would have underlain the posteromedial-most corner of the anterior crus, including the processus tubarius, which may be quite large in some forms (e.g., F:AM 102387). As in the other nimravids, the end of the anterior crus lies just posteromedial to the postglenoid foramen.

In most specimens, a large processus tubarius extends medially from the anterior crus, along the anteromedial margin of the epitympanic recess. This process is broader than in Dinictis or Nimravus, and much like that of Nimravus in having an oblong bulb at its medial end.

The posterior crus is short, resting in a small concavity in a vertical ridge on the anteromedial edge of the mastoid process, visible in F:AM 62078. In F:AM 69417, the crus is clearly in place, articulating with this ridge. A much broader and more co-ossified suture unites the posterior crus with the anteromedial edge of the mastoid process in F:AM 102387, apparently contributing in this specimen to the anterior wall of the facial canal. Immediately lateral to the dorsal tip of

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the posterior crus, in the squamosal roofing the external auditory meatal canal, there is sometimes a shallow but well defined fossa, in the position of the much deeper suprameatal fossa of the Procyonidae. This fossa is present in five of the specimens I studied in detail, questionably present in a sixth (the posterior crus is displaced in AMNH 82440 and together with matrix appears to be obscuring such a fossa), and clearly absent in the seventh, the largest (F:AM 102387).

Ventral and medial expansion of the ectctympanic occurs anteriorly, producing a brcadened plate. Posteriorly, the amount of expansion lessens until at the posterolateral corner of the ectotympanic, the tympanic ring is only slightly expanded, and the ventral edge flattened horizontally instead of vertically expanded. As in more complete ectotympanics in Dinictis and Nimravus, the posterior part of the ventral edge in F:AM 69417 does appear nearly complete, and does show a broadened facet as if it articulated with a cartilaginous bulla. F:AM 102387 also has a broadened ventral margin on the posterior section of the ectotympanic, but in this case the margin is sulcate.

Anteromedially, the ectotympanic is expanded horizontally, forming a bony trough for the auditory tube, and thereby the anterior margin of the bulla. In F:AM 69417, the ventrally expanded plate of the ectotympanic

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does not extend the entire length of this ectotympanic process, thus leaving a slight emargination anteriorly as in Dinictis or Nimravus. The end of the osseous auditory tube in F:AM 69417 is rather produced, suggesting a styliform process, but is directed more ventrally than is typical. In this specimen, the anteromedial-most part of the ectotympanic is separated from the basisphenoid wall medially by what appears to be a fragment of the anterior half of entotympanic. Because of damage in this region, however, a basisphenoid contribution to the bone between the medial wall and the osseous canalis musculotubarius cannot be conclusively ruled out.

In contrast, the anteromedial-most extent of the ectotympanic in AMNH 82440 abuts a small lateral process from the basisphenoid (see Figure 38). This section of the ectotympanic is greatly emarginate, a condition exaggerated by the ventral extension of the anterior tip. This extension does not appear so clearly to be a styliform process because it forms instead the lateral wall of a vertical canal mostly enclosed in basisphenoid and presumably for an anastomotic ramus from an ascending pharyngeal artery running up to the internal carotid foramen. This bony trough or canal is very well marked in AMNH 82440 (Figure 38), showing that its contents were headed anteriorly just behind the anterior margin of the basisphenoid buttress at the anterior end of the bull,

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then turned sharply dorsally and even posteriorly to run in a channel on the ventral surface of the epitympanic wing of the sphenoid, toward the internal carotid foramen. F:AM 69417 similarly shows a foramen defined by a curved margin in the sphenoid and the anterior surface of the bullar wall (either a basisphenoid projection or a piece of entotympanic as mentioned above), again heading dorsally into the channel in the sphenoid.

All specimens with this epitympanic wing of the sphenoid exposed show a well marked sulcus just medial to the groove for the pterygoid nerve, and ending ventrally in a cul-de-sac just dorsal to the buttress of the basisphenoid. In the very large specimen numbered F:AM 102387, the anterior part of the bulla is more complete, and the ectotympanic abuts the inturned edge of the buttress of the basisphenoid. Here the trough for the auditory tube has deepened, so the ventral lip is drawn down almost into a spout or lip like that of a pitcher. Dorsally the auditory tube would have passed through this aperture, but ventrally it appears to be shaped to accomodate a fairly large vessel coming from below and diving up and posteriorly to the channel in the basisphenoid above the entotympanic.

Entotympanic.--No specimen of Hoplophoneus yet discovered has a completely enclosed, fully ossified bulla. Even in specimens that appear to be otherwise well

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preserved, such as F:AM 69417 which has hyoid elements preserved, there are not even fragments ventrally that could be interpreted as the remains of a fragile bulla. Instead, the pieces of entotympanic that are preserved form only dorsomedial and posterior margins of the bulla. These pieces are thick and double-layered: as in Dinictis and Nimravus, thin sheets of bone sandwich a thicker layer of matrix and open cancellous bone.

In F:AM 69417, part of the anterior end of the entotympanic is preserved, but not enough of the anterior margin to demonstrate conclusively whether a partial partition or septum (as in Dinictis) was or was not present. In F:AM 102387, the anterior margin of the entotympanic curves laterally where it is preserved dorsally. Ventrally it is missing, and the ectotympanic that appears to have abutted the ventral portion of the entotympanic is left standing, looking initially like a partial septum. However this is the posteromedial wall of the osseous canalis musculotubarius, and would be outside the bulla at this point were the entotympanic more complete.

The medial entotympanic wall in F:AM 69417 and AMNH 82440 displays no trace of a channel or canal for a medial internal carotid artery. Instead, more laterally, there is a short tube in the entotympanic of AMNH 82440 for a laterally placed internal carotid artery (Figure 38). A

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distinct foramen is present in the same position in the posterior wall of F:AM 69417's entotympanic.

The entotympanic in both F:AM 69417 and AMNH 82440 forms medially a long dorsal shelf, overlapping the promontorium and projecting backwards over the posterior lacerate foramen. (Since Hough's specimens did not have fully ossified bullae preserved either, I presume that it is this dorsal shelf to which she referred when she said "but the floor is flattened giving a pillbox shape" (1953: 99).) In neither F:AM 69417 nor AMNH 82440 is the posterior wall preserved laterally, but there is a large, smooth, slightly flattened face on the medial side of the mastoid process in both specimens, with a well defined ventral edge on the exoccipital, forming a facet against which an ossified entotympanic might have lain. (The ventral limit of this facet on the side of the mastoid process is not nearly so clear.) However, in contrast to the implications of such facets, the broken edge of the dorsal portion of the entotympanic present in F:AM 69417 implies by its angle and separation from the adjacent exoccipital that the remainder of the posterior entotympanic would have been ventrally directed and would not have been closely appressed to the neighboring mastoid or exoccipital elements. Indeed most of the remaining specimens show less clear cupping of a bullar space by the adjacent bones.

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The other extreme is also preserved, however in F:AM 102387. (I do not use the name assigned this specimen in the collection because F:AM 62022 is also labelled H. occidentalis and is much smaller and with a very different auditory region. The two are very unlikely to be conspecific, and I do not know with which, if either, the name should go.) In the very large nimravid represented by F:AM 102387, the auditory bulla was actually cupped by the expanded mastoid process. The entotympanic in this specimen is very thick, and curves completely around the posterior margin to join the hyoid process anteromedialy to the facial canal. A crista extends from the posterior wall of the entotympanic to the promontorium, a feature not found in any of the other Hoplophoneus, nor in Nimravus or Dinictis. What appears to be the posterior end of a canal lying between the inner and outer skin of the entotympanic along the medial side of the bulla is likely to be an artifact of previous incomplete and hasty preparation; additional careful preparation is needed on this specimen to resolve this question.

Tympanic Roof

The auditory cavity in Hoplophoneus varies from moderately deep and laterally compressed (e.g. F:AM 62022, 62078, 69417) to extremely deep and compressed (AMNH 1406, 82440, F:AM 102387). In both cases, the anterior-most

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part of the auditory region is so far anterior that it is on a level with the postglenoid process.

Petrosal.--The petrosal is rather small and compact in this genus, with a small, bulbous promontorium. At least one-third the width of the petrosal is overlapped by the medial entotympanic, as is a variable but large part of the promontorium posteriorly. AMNH 1406 shows that the basioccipital abuts the medial margin of the petrosal along the posterior half of that margin, roofing over the posterior section of the petrobasilar canal. Posterolaterally, the prominent caudal process of the petrosal projects ventrally from a flattened region of the petrosal, medially walls off the facial canal, and abuts the hyoid process from the mastoid (shown clearly in both AMNH 82440 and F:AM 69417).

The aperture of the cochlear fossula faces posterolaterally and rather ventrally. In some specimens (e.g. AMNH 82440 and F:AM 69417), a shallow channel across the posterior face of the promontorium runs into the medial wall of the cochlear fossula. In others, no such channel is present. The vestibular fenestra faces anterolaterally, and is positioned rather dorsally, as in Dinictis and Nimravus.

Faint longitudinal grooves are visible across the promontoria of AMNH 82440 and F:AM 69417. The grooves in these two specimens appear to swing medially on the

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anteroventral face of the promontorium. In contrast, a broad, shallow sulcus on the promontorium in F:AM 102387 is positioned very far laterally and is aimed directly at the vestibular fenestra, as if for a stapedial artery. (This channel is in line with a peculiar channel through the medial margin of the large mastoid process.) In this specimen, there is also a more medial, but much less well defined, groove on the promontorium.

Finally, in F:AM 62078, there is a small, very sharp sulcus aimed from the posterior margin of the petrosal across the aperture of the cochlear fossula, and continued by a sulcus between the latter and the vestibular fenestra, as if for a stapedial artery. (Farther on, in the anterior wall of the epitympanic recess is a small foramen as if for a superior ramus of the stapedial artery.).

AMNH 82440 and F:AM 62078 show little or no development of an epitympanic wing medially from the petrosal, leaving a very wide piriform fenestra between the petrosal and sphenoid. Laterally, the tegmen tympani abuts the squamosal, and contains on its ventral surface a nearly round, moderately deep, and very well defined fossa muscularis major. Farther laterally, the petrosal contributes a small medial portion of the roof of the moderately sized epitympanic recess.

Sphenoid.--A large epitympanic wing of the sphenoid

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overlies the anteromedial ectotympanic. This wing has a smooth, finished posterior edge in AMNH 82440, strongly indicating that the large piriform fenestra in that specimen is not an artifact of either preservation or preparation.

Several faint grooves run across the ventral surface of this epitympanic wing. A small but distinct pterygoid groove lies lateral tc a larger, more open channel running from the foramen in the basisphenoid at the anteromedial corner of the bulla (Figure 38) to the medial portion of the piriform fenestra. The pterygoid groove is presumed to have carried the pterygoid artery or nerve or both. I think the larger channel may have carried an anastomotic ramus from an ascending pharyngeal artery, or comparable vessel, through the internal carotid foramen (here confluent with the piriform fenestra) to the internal carotid circulation.

Squamosal.--The anterior wall of the tympanic cavity is completed laterally by the squamosal. The greater part of the epitympanic recess is contained within the squamosal, including the deeper secondary pocket for the posterior crus of the incus and the suspensory ligament. In F:AM 62078, dissected so that the lateral part of the tympanic roof as well as the intracranial surface is more visible and more easily prepared, the secondary pocket within the epitympanic recess is clearly visible. There

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is also a small foramen, of approximately the same caliber as the foramen and sulci for the middle meningeal arteries intracranially; this foramen could be for the superior ramus of the stapedial artery if one were present in the sulcus across the promontorium.

In the posterior half of the dorsal roof of the tympanic notch, a shallow depression in most specimens suggests the presence of a suprameatal fossa. This can be clearly seen in F:AM 62078, dorsolateral and anterior to the pit for the posterior crus of the ectotympanic, as well as in F:AM 69417, in which the posterior crus appears to be complete. This latter specimen provides evidence that rules out the possibility of this depression being part of a larger contact between the posterior crus and the mastoid as is the case in Dinictis.

The lateral flange of the squamosal dorsal to the external auditory meatus is slightly broader in Hoplophoneus than in Dinictis or Nimravus, and much broader in the large, aberrant form represented by F:AM 102387. (This increased width is not simply associated with increased sabertoothy and pedestalling of the glenoid fossa, or simply increased size, because Barbourofelis is even more extreme in these features and yet does not show the broadening of the squamosal flange.)

Principal Tympanic Spaces and Foramina

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Although difficult to estimate because of the incomplete preservation of the entotympanic, the total bullar volume appears to have been rather small for the size of the skull. This estimate is based on the inclination of the ectotympanic plate and the apparent lack of inflation posteriorly in AMNH 1406 and F:AM 69417. (See earlier discussion of the entotympanic on p. 272.)

Tympanic cavity.--In spite of the apparently small bullar volume, the tympanic cavity proper is moderately large because of the depth of the auditory cavity, especially so in F:AM 102387.

Epitympanic recess.--This circular concavity is deeper in Hoplophoneus than in Dinictis or Nimravus, and to a greater degree--almost entirely--contained within the squamosal. A deeper secondary pocket at the edge of the squamosal probably contained the posterior crus of the incus and its suspensory ligament. In the suture between the petrosal and squamosal, F:AM 62078 displays a small foramen in an appropriate position for the superior ramus of a stapedial artery. A corresponding foramen into the grooves for the meningeal arteries has been only tentatively recognized on the dorsal surface of the squamosal in this specimen).

Posterior lacerate and adjacent foramina.--The posterior lacerate foramen is positioned quite laterally along the posterior margin of the auditory cavity. Its

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anterior margin is defined dorsally by the posterior rim of the petrosal and ventrally by the entotympanic, and its posterior margin by the occipital bone. Two distinct channels are present in the occipital wall of this foramen in AMNH 82440--a lateral one through which the canal for the sigmoid sinus opens, and a medial one opening directly from the interior of the braincase. Presumably the lateral channel transported the contribution from the sigmoid sinus to the internal jugular vein, whereas the medial channel carried nerves IX, X, and XI.

Medial to the posterior lacerate foramen and within the basioccipital is the posterior end of the petrobasilar canal. As in Nimravus and Dinictis, this foramen has been misidentified for the last century as the posterior opening of the carotid canal (e.g., Cope, 1880a; Matthew, 1910; Hough, 1953; etc.). AMNH 1406 shows that the channel extending anteriorly from this foramen is excavated within the lateral wall of the basioccipital well dorsal to the ventral surface of the promontorium. Posteriorly the channel is roofed by a flange of basioccipital that abuts the posteromedial edge of the petrosal, walled laterally by a ridge in the occipital, and floored by entotympanic. More anteriorly, the channel passes even more medially to the dorsal surface of the basioccipital. This path is characteristic of a petrobasilar canal for the inferior petrosal venous sinus.

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The hypoglossal foramen is positioned behind the posterior lacerate and petrobasilar foramina, posterolateral to the petrobasilar foramen and posteromedial to the posterior lacerate foramen. This foramen is directed quite ventrally and for that reason appears well separated from the posterior lacerate foramen. However F:AM 69417 displays in its right auditory cavity an odd, smooth trough between the posterior lacerate and hypoglossal foramina, as if there had been some soft tissue connection between the contents of the two canals.

Internal carotid foramen.--Because of the large piriform fenestra, there is no definable osseous internal carotid foramen. If my identification of the canal on the ventral surface of the sphenoid is correct--that it carried an anastomotic ramus from an ascending pharyngeal artery to the internal carotid circulation--then the posterior end of that channel gives an indication that the internal carotid foramen would have been medially placed within the membrane roofing the gap, as would be expected.

Posterior carotid foramen.--As noted above, the foramen that is identified elsewhere in the literature as the posterior carotid foramen is not; it is the petrobasilar foramen. None of the specimens of Hoplophoneus examined in detail has any trace of a medial carotid canal or channel. (I do not believe the hole dug

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within the entotympanic in F:AM 102387 to be good evidence until corroborated by more careful preparation.) The true posterior carotid foramen, according to my identification, had apparently not been seen in a specimen prior to this study: preparation of AMNH 82440 revealed a short tube laterally placed in the dorsal half of the posterior wall of the entotympanic, running in an anterior-posterior direction (Figure 38). F:AM 69417 has a small foramen in a comparable position, much like that seen in Dinictis (AMNH 6937).

Even slightly more laterally placed is the foramen through the medial margin of the greatly expanded mastoid process (really including the paroccipital process) seen in F:AM 102387. This foramen appears to be in line with the sulcus on the promontorium (extrapolating from the right side, on which the foramen is preserved, to the left which is completely enough prepared to see the ventral surface of the promontorium.)

Other foramina and fenestrae.--At the anteromedial corner of the auditory region, a foramen is formed by the basisphenoid and bullar elements. In AMNH 82440, the channel and foramen are well defined in the basisphenoid and almost totally enclosed by that element; the anteromedial end of the ectotympanic may contribute to the anterior margin of this foramen (Figure 38). In F:AM 69417, the channel in the basisphenoid is shallower, and

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partially walled posterolaterally by entotympanic. And in F:AM 102387, the ventral entrance to this canal appears to be entirely within a trough in the ectotympanic. I interprete this foramen to be for an anastomotic ramus of an ascending pharyngeal artery or comparable artery.

As in the other nimravids, the foramen ovale of Hoplophoneus is sunk in a common oval depression with the posterior aperture of the alisphenoid canal. Hough (1953: 99) noted that such an arrangement of the two foramina was exactly like that in Canis, except that the orientation of the common fossa is more transverse in the latter. The postglenoid foramen is proportionally rather small (contrary to Hough's observations), and is medially positioned.

The apparent stylomastoid foramen is situated rather dorsally, relative to the elongate mastoid process, and posterior to the insertion of the hyoid apparatus. It is not clear whether or not in life a longer canal would have been formed by additional bullar elements, perhaps producing a more ventral stylomastoid foramen.

No clear canal is formed by the caudal process of the petrosal for the auricular branch of the vagus nerve, nor is a channel clearly visible in the posterior wall of the auditory cavity. Some grooving at the base of the mastoid process in F:AM 69417 may represent such a channel.

Adjacent Cranial Morphology

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Basisphenoid.--As in the other nimravids, the basisphenoid in Hoplophoneus usually forms a triangular buttress at the anteromedial corner of the bulla, in place of the anteromedial process from the entotympanic typical in other carnivorans. (No such buttress is present in F:AM 62022, although this is a rather typical Hoplophoneus in other respects.) Hoplophoneus is unusual, however, in that the medial channel in the epitympanic wing of the sphenoid sometimes ends ventrally in a fairly well defined foramen in the basisphenoid (described above). Just posterior to this foramen in AMNH 82440, there is a very small canal through the edge of the basisphenoid that perhaps carried a medially directed dorsal branch from either the ascending pharyngeal artery or its anastomotic ramus.

Basioccipital.--The lateral margins of the anterior basioccipital are produced into sharp, vertical flanges. These are pronounced, producing a trough-like basisphenoid. Because of variable preservation, it is not clear how much individual variation occurred in this feature.

Lateral margin of auditory region.--Distinct pedestalling of the glenoid fossa and hypertrophy of the mastoid process produces a tall and narrow tympanic notch in Hoplophoneus. A forward inclination of the mastoid process leaves a slightly wider notch dorsally than

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ventrally. The postglenoid process is well developed and ventrally directed.

The very large mastoid process is, like the pedestalling of the glenoid fossa, a feature associated with increasingly exaggerated sabertoothy. In Hoplophoneus, the usual squared-off rugose ends of the mastoid processes are often slightly anteriorly or laterally as well as ventrally directed. The result of this orientation can be seen in AMNH 1406, which is preserved with the jaws intact and articulated. Each end of the mastoid process clearly faces towards the corresponding angular process of the lower jaw and the ridge extending anteriorly from that angular process. This is of interest because the angular process is directed quite laterally, so that the bottom of the jaw has a distinct bend in it, and the articular condyle is entirely to the medial side of the posterior margin of the ramus. One obvious hypothesis was that this peculiar mandibular morphology was related to the need for very accurate control of lateral position as the mandible closed so that the anterior end was positioned correctly between the saberlike canines.

The hyoid process projects from the ridge down the anteromedial corner of the mastoid process, often abutting the caudal process of the petrosal medial to the facial canal. Both AMNH 82440 and F:AM 69417 clearly show a

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small pit for the insertion of the cartilage or ligament of the dorsal-most element (tympanohyal in these forms?) of the hyoid apparatus. This pit is on the end of the hyoid process, positioned just ventral to the aperture of the cochlear fossula, and immediately anterior to the stylomastoid foramen.

Although the posterolateral corner of the basicranium is rugose and squared-off as if good-sized muscles attached there, the paroccipital process itself is reduced in Hoplophoneus. AMNH 1406 exhibits short, broad processes, posterolaterally (and not ventrally) directed. F:AM 69417 has a small leaf-like edge preserved on the right side, but dorsal to that a broad, projecting, rugose area. In my observations of individuals of this genus, the paroccipital processes were not as well developed as Hough (1953: 99) described them; I found a great reduction in the distinctness and elongation of the paroccipital processes as the mastoid processes increased and the ear region became laterally compressed. The extreme among these specimens is seen in F:AM 102387, in which the mastoid processes are so large and thick, they appear to have taken over the whole region from the level of the hypoglossal foramen medially, to the side of the skull laterally. Paroccipital processes are represented by some rugosities on the posterolateral corner of these mastoid processes.

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Intracranial Morphology

Removal of the matrix from inside the braincase (on the left side) of AMNH 82440 and preparation of the separated auditory region of F:AM 62078 permits description of the intracranial auditory morphology of Hoplophoneus.

Petrosal.--As in Dinictis, the petrosal of Hoplophoneus is rounded, lacking both a sharp petrosal crest and an elongate rostral apex. This condition is unlikely to be an artifact of preservation since both specimens (AMNH 82440 and F:AM 62078) present the same smoothly sculptured dorsal surface in place of the crest, and similarly shaped rostral apices, both shallowly grooved.

Hoplophoneus has an even smaller anterior petrosal face than seen in Dinictis, again little covered, if at all, by squamosal. The prominence at the anterior end of the petrosal, above the sulcus for the trigeminal nerve, is more pronounced and pyramidal. Posterior to this prominence and sulcus, the internal auditory meatus is of moderate size, roughly oval in shape. One foramen above and two below are separated within this meatus by a deeply set transverse crest. The area of the petrosal immediately around the internal auditory meatus appears swollen: beyond this torus, a gently concave shelf-like expanse of petrosal extends posteriorly and dorsally.

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This shelf is relatively smooth in F:AM 62078, but pitted by a small excavation in AMNH 82440. (The dorsal part of this shelf is broken in AMNH 82440, revealing the anterior semicircular canal.) On the dorsal half of the cerebellar face, there is no clear subarcuate fossa, only the shallow, elongate depression beyond the edge of the swollen torus surrounding the internal auditory meatus.

The hiatus facialis is on the broad anterior edge of the petrosal, opening immediately into the piriform fenestra. The slit-like foramen that may be identified on the basis of its general location as the opening of the osseous canal for the vestibular aqueduct is slightly more than two millimeters anterior to the posterior edge of the petrosal, right at the edge of the swollen torus around the internal auditory meatus. The slitlike aperture would have housed the endolymphatic sac. Ventrally, the aperture of the canal for the cochlear aqueduct is similarly placed, at the bottom edge of the posterior shelf, a few millimeters anterior to the posterior-most edge of the petrosal. From the ventromedial side in F:AM 62078, a small notch ends at the opening of the bony canal for the cochlear aqueduct, in the anterior edge of the portion of the posterior lacerate foramen identified above as transmitting specifically the three cranial nerves. In F:AM 62078, in which the posterior edge can be most clearly seen, I find no equivalent of the small,

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unidentified foramen seen in Dinictis. There is a small pit in this specimen at the posteroventral corner of the petrosal, on the edge, but I interpret this to be a small, matrix-filled, broken area rather than a well defined foramen.

Intracranial channels.--A frontal section removing the top of the braincase of AMNH 82440 revealed a cross section of a large canal for a transverse venous sinus, completely enclosed by squamosal. A large ridge of squamosal extends tangentially to the anterodorsal margin of the petrosal, presumably enclosing a canal for a superior petrosal venous sinus, since there is present a moderately sized postglenoid foramen.

At the dorsal apex of the petrosal, a large sulcus for the sigmoid venous sinus opens posteriorly from the ventral end of the transverse sinus. This channel is deeply incised into the squamosal and occipital, and into any dorsal process of the pars mastoidea present (the sutures in this area are not distinguishable). Half-way down, a foramen opens into the floor of the channel from a posterodorsally directed canal. Because of the thickness of the occipital bone in this area, the development of the nuchal crest, and the oblique angle of the channel through the bone, the channel itself is several millimeters long and the external opening of this channel, termed by Cope (1890) the mastoid foramen, occurs distinctly dorsal to

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the level of the internal foramen. Externally, the mastoid foramen is located rather laterally, positioned just above the level of the top of the occipital condyles and immediately beneath the nuchal crest.

On the external lateral wall of the braincase, a large foramen corresponds in position to Cope's (1890) postparietal foramen. None of the available skulls permit passage of a bristle, but it is clear in the cross section of AMNH 82440 that this foramen is located over the canal for the transverse venous sinus. In lateral view, the foramen is positioned slightly more dorsally than in Dinictis.

The condyloid canal is long: its anterior end is a foramen in the posterior wall of the sulcus for the sigmoid sinus and its posterior end is a foramem well back in the lateral wall of the foramen magnum.

A bar of bone forms a medial wall over the ventral-most end of the sigmoid sulcus, separating it intracranially from the internal posterior lacerate foramen. In ventral view of AMNH 82440, the end of this short canal for the sigmoid sinus can be seen immediately adjacent to the posterior lacerate foramen at the level of the posterior edge of the petrosal. The two passages become confluent ventral to this point, and exit the skull through the external posterior lacerate foramen, between the entotympanic and exoccipital. A small ridge on the

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exoccipital wall of the posterior lacerate foramen, continuous dorsally with the bridge of bone across the sigmoid sinus channel, partially separates the common passage, defining a channel laterally for the vein and medially for the nerves. (A larger, much wider ridge medially separates the petrobasilar canal in the ventral surface of the basioccipital from the posterior lacerate foramen: see description above.)

A well defined sulcus on the intracranial surface of the exoccipital runs posteriorly from the internal posterior lacerate foramen, ending immediately above the internal hypoglossal foramen. This channel has very distinct margins, anteriorly curving ventrally into the posterior lacerate foramen. The posterior extent of the channel is less clear, because the sulcus is continuous with the sharpest part of the curve of the foramen magnum, between the posterior opening of the condyloid canal and the internal hypoglossal foramen.

A shelf of basioccipital (and perhaps basisphenoid--the position of the suture is unclear) roofs the petrobasilar canal nearly the entire length of the petrosal. Posteriorly, the basioccipital bears large flanges, descending on the medial side of the canal, but laterally is produced into only a slight ridge ventrally; the floor and lateral wall of the canal are formed by the entotympanic. The depth of incisure into the

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basioccipital increases anteriorly so that the canal is roofed and floored by basioccipital, and bounded laterally by the petrosal. Grooving or channelling on the medial margin of the petrosal is slight, due to the great extent to which the petrobasilar canal is enclosed by the basioccipital. F:AM 62078 shows a shallow channel at the anteromedial corner of the petrosal, on the ventral surface, and an even shallower one on the ventral edge of the medial surface. In AMNH 82440, the medial channel is the more distinct. (The petrosal in this specimen is interpreted as having been slightly displaced dorsally at the anteromedial corner; the identification of this channel as the lateral wall of the petrobasilar canal is dependent on the accuracy of this interpretation.)

An elongate oval foramen marks the anterior opening of the petrobasilar canal into the cranial cavity (Figure 39), at the confluence of the inferior petrosal sinus with the cavernous venous sinus. Posteriorly, the petrobasilar foramen is not visible intracranially, being completely roofed over by basioccipital.

An anastomotic ramus from the internal maxillary branch of the external carotid artery to the middle meningeal artery may be inferred from the groove in the squamosal, leading from the posterodorsal margin of the foramen ovale posterodorsally to the meningeal sulci on the internal surface of the braincase. In contrast to

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F:AM 62078 and the Dinictis specimen, AMNH SD 230-4152, the other specimen of Hoplophoneus (AMNH 82440) has a rather large channel running posterodorsally from the foramen ovale, dorsal to the channel for the trigeminal nerve, and extending to the base of the squamosal ridge thought to enclose the superior petrosal sinus. A small channel to the groove for the middle meningeal artery branches off from the dorsal edge of this larger channel.

EUSMILUS

Little can be said about this taxon at the present time because most of the known specimens are under study by another investigator in another part of the country. One skull, however, AMNH 6941, was available; its right auditory region was therefore prepared for study and comparison, and may be briefly described here.

Tympanic Floor: Auditory Bulla

The tympanic ring is entire although ventral portions of the ectotympanic may have broken away. Much as in the other nimravids, the broadened horizontal anterior crus extends over the top of the tympanic notch to within a few millimeters of the short, vertical, posterior crus. The annulus is about the same width posteriorly as anteriorly,

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so the planes of the crista tympanica and the outer rim of the external auditory meatus are parallel. This plane is very nearly vertical, perhaps tipped 10 to 15 degrees (ventral edge directed slightly posteromedially). The angle of the ring from the sagittal plane is close to 45 degrees, however. Also as in the other nimravids, the slightly oval meatus is much larger diameter than the tympanic notch is wide, which, combined with the angle, causes the ring to overlap the base of the pedestal above the glenoid fossa and the meatus thus to face anterolaterally into the base of the postglenoid process.

The broadened anterior crus spreads out around the postglenoid surface above the postglenoid foramen, but does not appear co-ossified with the squamosal. A very thin processes tubarius projects posteromedially from the anterior crus, along the posterior margin of the anterior auditory sinus to the edge of the fossa muscularis major. The posterior crus is neatly appressed to the anterior surface of the processus hyoideus.

Adjacent to the crista tympanica, the internal surface of the ectotympanic is concave in an even, narrow torus. The posterior portion of the ventral edge is broadened but still irregular. Anteriorly, however, a rather smooth edge extends forward beneath a plate of ectotympanic to end in a process correctly positioned to be a styliform process. The internal face of this

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ectotympanic has a vertical ridge midway along it, and a roughened surface on the half anterior to that ridge, as if it abutted a curve of entotympanic around the front of the tympanic cavity as has been observed in Dinictis and Hoplophoneus.

No entotympanic remains on either side in AMNH 6941, but that the element was present is clearly indicated by the large vertical facets on the lateral faces of the basioccipital or basisphenoid and on the flattened ventral surface of the caudal process of the petrosal.

Tympanic Roof

The auditory region and tympanic cavity is laterally compressed and deeply recessed above the level of the basisphenoid. The petrosal is an elongate mound, with the aperture of the cochlear fossula facing almost directly posterolaterally, and not at all ventrally. Through the external auditory meatus, a round fenestra vestibuli may be seen facing anterolaterally. A shallow but very distinct groove runs across the promontorium, from the posterior margin just medial to the cochlear fossula, forward and curving gently medially to aim directly at the internal carotid foramen within the basisphenoid.

Anterior to the promontorium, the roof of the tympanic cavity proper is very compressed. The facial foramen is directly dorsal to the vestibular fenestra,

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right at the posterolateral edge of the fossal muscularis major--a much more typical position for the foramen than that seen in Dinictis or Hoplophoneus. From the facial foramen, the sulcus turns posteriorly past the end of the promontorium to the base of the mastoid process, then abruptly ventrally through a ring formed by the mastoid laterally, the hyoid process anteriorly, and medially a very long extension of the caudal process of the petrosal that curves down and anteriorly to meet the hyoid process. The channel down the medial face of the mastoid is not particularly distinct, nor is there clear evidence of how far ventrally the entotympanic formed a medial wall and a vagina processus hyoideus.

The fossa for the origin of the tensor tympani muscle is large and deep, recessed above the promontorium, and contained entirely within the epitympanic wing(s) of the petrosal. Lateral to the fossa muscularis major, the epitympanic recess is of moderate size in diameter but generally rather shallow. I do not see any distinctly outlined deeper pocket for the posterior crus of the incus, but the posterior part of the recess appears more deeply excavated so that the recess is not a hemisphere as in other nimravids. There do appear to be two very small foramina in the posterior half of the recess, one in the petrosal and one in the squamosal.

Anterior to the fossa muscularis major, a narrow

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anterior auditory sinus (see the description of Nimravus) extends forward into the squamosal above the medial end of the glenoid fossa and pedestal. The tympanic cavity is so compressed that this sinus is dorsal to the anterior edge of the tympanic ring. Whether this sinus is entirely in the squamosal or is partly or entirely in an epitympanic wing of the sphenoid is not clear, because I am unable to decide with certainty which divisions are sutures and which fractures.

Principal Tympanic Spaces and Foramina

Because of the depth of the cavity, the degree of lateral compression, and the lack of evidence about the ventral extent of bullar elements, it is not really possible to estimate the relative size of the hypotympanic sinus. The tympanic cavity in the restricted sense is certainly narrow but deep, and looks like a very similar volume to that of Hoplophoneus.

The posterior portion of the basicranium is largely missing, so the condition of the posterior lacerate foramen, or the presence of a petrobasilar foramen or a posterior carotid foramen, can not be determined.

Anteriorly, an internal carotid foramen is very well defined, so deep in a notch that is is almost completely surrounded by the basisphenoid. Immediately lateral to this foramen is a groove leading to the pterygoid canal,

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but no other channel, such as one that might be identifiable for an anastomotic ramus from the ascending pharyngeal artery. Posterior to this epitympanic wing of the sphenoid, the piriform fenestra is confluent medially with the anterior part of the basicapsular fenestra.

As in the other nimravids, the foramen ovale is sunk in a common fossa with the posterior alar foramen. Preservation is not good enough to determine the disposition of foramina in the Glaserian fissure. The postglenoid foramen is not as large as that in Dinictis but is still of moderate size, indicating that the external jugular was a significant part of the cerebral venous drainage.

The section of the facial canal preserved has been described above. Lateral to the caudal process of the petrosal is a good-sized channel running to the dorsal part of the facial canal, presumably for the auricular ramus of the vagus nerve.

Adjacent Cranial Morphology

Most or all of the basioccipital is missing. The piece of medial element remaining, probably basisphenoid, is very thick in cross section: on a skull no longer than 12 cm, the bone is 0.6 cm at the thinnest point. From the angle of the margins remaining, it may also be inferred that the base of the skull was laterally compressed

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between the bullae. At the anteromedial corner of the auditory region, there is no evidence of an anteromedial process from the bulla, but instead, the basisphenoid is produced ventrally into buttresses that continue posteriorly as ventral flanges.

Along the lateral margin, the glenoid fossae are positioned on the end of deep pedestals, and the mastoid processes are elongate and directed forwardly, forming a tall, narrow tympanic notch. The amount of squamosal contribution to the mastoid process is not determinable on this specimen. The paroccipital processes are apparently reduced even further than in Hoplophoneus, to mere rugosities on the posterior surfaces of the mastoid processes.

Intracranial Morphology

Part of the intracranial surface of the auditory region has been prepared on this specimen. The cerebellar face of the petrosal is rather rounded in overall outline, much like that of Dinictis or Hoplophoneus. Also like Dinictis, there is a distinct sulcus in the anterior part near the apex, clearly interpretable as a sulcus for the trigeminal nerve. There is a shallow subarcuate fossa, and a oval internal acoustic meatus. From the rather posterior angle of view, the anterior edge looks rounded, as if no distinct crista petrosa were present. Certainly

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there is no development of an osseous tentorium overhanging the petrosal.

Much of the sigmoid sulcus is broken posteriorly, but the remaining portion continues ventrally back of the petrosal, indicating that at least this part of the posterior lacerate foramen was positioned quite laterally. It was possible at one stage during preparation to see the cross section of a sulcus in the side and dorsal surface of the posterior-most remaining piece of basisphenoid or basioccipital. This corner was lost during subsequent preparation, but had indicated part of a rather dorsally positioned sulcus, as would be expected so far anteriorly.

Dorsal to the petrosal on the intracranial wall, one can see not only the ventral end of the canal for the transverse sinus from above, but also the posterior opening of the superior petrosal canal, thus corroborating the evidence of the postglenoid foramen that some cranial drainage was effected via the external jugular system in Eusmilus.

BARBOUROFELIS

Based in detail on F:AM 61871 (1), F:AM 61876 (1), F:AM 61891 (internal), F:AM 61895 (l, r, & internal), F:AM 61961 (l & internal), UF 23796 (l, r, & internal), UF

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24432 (l & internal), and UF 36867 (l, r, & internal).

Tympanic Floor: Auditory Bulla

Numerous specimens of Barbourofelis display complete, fully ossified auditory bullae (e.g. F:AM 61895 and F:AM 61876). In those specimens in which the bullae are incomplete, this condition is clearly due to breakage. The bullae are large and very inflated, projecting ventrally as far as the end of the enlarged mastoid process or beyond.

In no specimen of Barbourofelis that I have seen is there any direct, conclusive evidence for an entotympanic ossification within the bulla. Externally there is no consistent sign of division or suturing. Baskin (1981: 126) noted in B. lovei a difference in appearance between the lateral surface of the bulla (rugose and pitted) and the medial surface (smooth), and interpreted the former as ectotympanic and the latter as entotympanic. UF 24432, referred to this species, displays a projecting ridge on the ventral surface of the bulla between these two surfaces. However, the ridge runs from a position medial to the bony channel for the auditory tube cartilage, in a posterior direction, and at the level of the mastoid process, curves medially. The roughened and pitted surface extends past the stylomastoid foramen and the insertion of the hyoid apparatus to the posterior surface

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of the bulla. This would present a very unusual shape for the ectotympanic, the posterior crus of which is presumed to have inserted on the anteromedial corner of the mastoid process; in modern carnivorans, in contrast to this situation, posterior expansion of the ectotympanic is accompanied by a great degree of medial expansion as well--the extreme case being exemplified by the hyaenids.

F:AM 61961 displays a line that might be interpreted as a suture, positioned laterally, well within the rugose portion of the bulla (indicated in Figure 40). However, if this is a suture, its anterior extent is not discernible. Furthermore, internally the crista tympanica extends much farther medially; the precise relationship of an entotympanic to such a restricted ectotympanic is thus unclear.

F:AM 61895 is a young individual (adult cheek teeth fully erupted but canines only beginning to erupt) with a fully ossified left bulla preserved. No definite ectotympanic/entotympanic suture is visible, but the lip of the external auditory meatus is swollen, in an even more narrow strip than in F:AM 61961. Again, the anterior extent of this possible division between an ecto- and entotympanic element is not visible. More medially, there is a very slight change in color and perhaps density of the bone; if this is the site of co-ossification, then the ectotympanic contributed about a third of the bulla, the

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anterolateral wall from the stylomastoid foramen and vagina processus hyoideus posterolaterally to the bony trough of the canalis musculotubarius. Anteromedially, there is a groove that separates a medial sliver of bulla from the main body of bulla: this might be interpreted as a nearly co-ossified rostral entotympanic. Such a hypothesis could be tested by dissection of this specimen to demonstrate the relationship of this element with the internal carotid foramen if one exists.

A swollen, very rugose lip ventral to the external auditory meatus is also present in F:AM 61871 and F:AM 61876. In both cases, the roughened surface continues medially and no clear suture line is visible.

Because of this conflicting and uncertain evidence about the medial extent of the ectotympanic, and even whether an entotympanic contribution to the bulla is present at all, the rest of this description will refer to the element constituting the bulla as "tympanic". This should not be taken to mean that I believe no entotympanic is present--only that I cannot distinguish between the two elements if both are present.

As a function of the great inflation of the bulla and its resulting bulbous shape, the external edge of the tympanic ring is oriented vertically (e.g. F:AM 61871, F:AM 61876, F:AM 61895) or nearly so (61), in a plane oriented from about 45 degrees (e.g. F:AM 61895) to about

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25 or 30 degrees (e.g. F:AM 61961, F:AM 61871, UF 24432) from sagittal. The anterior end of the oval external auditory meatus lies medial to the posterior wall of the long postglenoid process. Thus the external auditory canal is roughly cylindrical, but of a smaller maximum diameter than the external auditory meatus itself, and as in other nimravids, the meatus faces anterolaterally into the base of the postglenoid process.

Internally, the crista tympanica is positioned quite medially and anteriorly relative to the external edge of the tympanic ring. The large circle of the crista tympanica lies in a plane extending dorsolaterally to ventromedially, at an angle as large as 30 to 40 degrees from vertical. A distinct crista is visible in an entire circle, even dorsally. Thus, although the crura of the tympanic are co-ossified with the adjacent cranial elements, the crura may perhaps be inferred to meet and form a complete, ringlike tympanic (rather than a U-shaped one as was stated in Baskin, 1981). The straight or even emarginate portion of the crista dorsally is interpreted as the portion to which the pars flaccida of the tympanum was attached. A very regular semicircle is circumscribed by the rest of the crista, to the tympanic sulcus of which the pars tensa presumably was attached. A large processus tubarius extends posteromedially from the anterior crus, along the anterior edge of the epitympanic recess. This

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process varies in shape from long and narrow (e.g. F:AM 61961 or F:AM 61871) to broadened and flattened with a slight anterior hook (e.g. UF 24432).

The internal surface of the bulla curves smoothly from the floor of the bulla in a lateral, dorsal, and finally medial direction to the edge of the crista tympanica. Thus the tympanic ring is very thick and triangular in cross section, as shown diagrammatically in Figure 42. That this triangular section is solid bone is demonstrated by a broken piece of the tympanic ring among some fragments associated with F:AM 61895. Anteriorly, the tympanic remains thick beneath the bony channel for the cartilage of the auditory tube.

Medially, ventrally, and posteriorly, the walls of the bulla are thin, and clearly unilaminar, in sharp contrast to the double-layered entotympanics of Dinictis, Nimravus, and Hoplophoneus. In many specimens, three partial septa buttress these walls, easily seen in F:AM 61871 and UF 24432. One septum is immediately posterior to the tympanic ring and houses in part the bony channel of the facial canal. The crista extends from, ventrally, the level of the center of the medial face of the mastoid process to, anterodorsally, the lateral-most point of the promontorium. This crista forms the anterior wall of a variably well defined sinus partially extending into the mastoid process. (The lateral extent of this chamber into

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the body of the mastoid is hidden in Figure 40 by the crista.)

A second crista runs anteriorly from the posterior lacerate foramen to the promontorium, ending just medial to the fossula cochleae. Enclosed within this crista are two to four channels of varying sizes. In UF 24432, the ventral-most pair comprises a large canal and immediately next to it a smaller canal, as if for the internal carotid artery (in a much more lateral position, clearly like a "promontory artery", rather than the typical carnivoran medial position) and an acccmpanying internal carotid nerve. The foramina more dorsally placed in UF 24432 and F:AM 61871 might be for rami of the tympanic nerve. (Opening externally in both F:AM 61871 and UF 24432, and the level of this crista, is the opening of the canal for the auricular branch of the vagus nerve, clearly oriented anterolaterally and not in line with the crista.)

This posterior crista is represented only by a low swelling and a few spicules of bone in F:AM 61876. Externally, only one large canal can be seen to run within this low crista to the promontorium; dorsal to its external opening is the posterior mouth of the anterolateral canal for the auricular branch of the vagus. This specimen has instead of this posterior crista, a thin oblique crista or shelf of bone from the center of the medial wall of the bulla.

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The third crista is in the anteromedial corner of the bulla, and is the one most remarked upon in the literature to date. Its dorsal edge runs from the medial side of the canalis musculotubarius posteriorly to the promontorium, but ventrally this crista curves mediad to form a horizontal septum. Thus its dorsal margin is much like the curve of the anterior end of the entotympanic in Dinictis. However, it is not clear how comparable these crista are because the limits of the ectotympanic are discernible in Dinictis whereas the number, definition, and extent of bony elements in the bullae of Barbourofelis are not known. Certainly the horizontal orientation of the ventral portion of this crista is unlike the condition in Dinictis.

Baskin (1981) also compared the cristae in the anteromedial corner of the bullae of both Dinictis and Barbourofelis with the partial septum seen in canids. As can be seen in Figure 48, the canid septum is larger and oriented very differently, sloping dorsomedially to ventrolaterally, and extending nearly to the level of the middle of the tympanic ring. Its dorsal edge lies medial and even extends posterior to the promontorium. The canid septum is formed by the incurved edge of the caudal entotympanic at the point of fusion between ecto- and entotympanics (Hunt, 1974); the composition of the crista in Barbourofelis is uncertain, as noted above (and the

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entotympanic, which in Dinictis forms the anterior partition, clearly does not fuse to the ectotympanic--see the discussion under Dinictis).

Baskin identified the body of the crista in UF 24432 as being composed of caudal entotympanic, and the small triangular piece of bone at the dorsolateral edge of the crista as possibly the rostral entotympanic, or possibly a broken fragment of the caudal entotympanic (Baskin, 1981: 127). Given the nature of the separation (it looks more like a break than a suture) and the absence of a distinguishable element in F:AM 61871 or F:AM 61876, I would not consider its identification as a rostral entotympanic well supported. The "bony canal" (Baskin, 1981: 127) in this element in UF 24432, when viewed under magnification through a break in the bulla where the hyoid probably inserted, can be seen to be a cross section of a cell in the highly pneumatized bone.

No definite styliform process is present in any specimen I studied, although the rugosity at the anterior edge of the bulla in UF 24432 might be interpreted as an ill-defined one. Unlike the condition in Dinictis, Nimravus, or Hoplophoneus, the bulla is produced into a distinct anteromedial process as is typical for many other carnivorans. This process is clearly seen in F:AM 61895, for example, which is young enough that the sutures in this region are still open.

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A thick medial wall to the canalis musculotubarius is formed by the anteromedial process. A thin layer of tympanic roofs this canal as well, but the anterolateral wall is incomplete, so that the rest of the canal is formed by the squamosal. Two large vessels or structures, at least, must have passed through this canal, as demonstrated by the partial division into a slightly larger barrel medially and a smaller one laterally. The anterolateral one is aimed at the processus tubarius, and thus may have merely conveyed the tendon of the tensor veli palatini muscle. There is no clear channel or foramen in the anteromedial corner of the bulla comparable to the foramen seen in Hoplophoneus, nor any groove or channel in the epitympanic wing of the sphenoid other than that for the pterygoid nerve (which can be clearly seen in UF 36867 or UF 23796, as can the pterygoid foramen at the anterior end of the canal in the later specimen), and therefore no direct evidence for a large anastomotic branch from an ascending pharyngeal artery as is inferred for the other three genera. However, UF 24432 has not only a larger internal carotid foramen than one would expect on the basis of the size of the posterior carotid foramen, but also a short but rather large diameter sulcus headed anteromedially out of that foramen on the floor of the cranial cavity. This, however, is extremely tenuous evidence from which to deduce the existence or prominence

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of any particular arterial supply to the intracranial circulation.

A very small blood vessel or nerve is indicted, however, by a very small subsidiary bony canal on the internal surface of the medial wall of the canalis musculotubarius in several specimens of B. lovei (UF 24432 and UF 24430) and the juvenile skull F:AM 61895, presumably a B. morrisi. The sulcus for the pterygoid nerve is distinctly lateral to this osseous canal, in the roofing sphenoid plate; the identification of this sulcus is of course confirmed by the termination of the sulcus in the pterygoid foramen. It is extremely difficult tc determine the posterior course of this tiny canal in the wall of the canal for the auditory tube. If one looks through the external auditory meatus in UF 24432 at the anteromedial corner of the tympanic cavity, one can see directly ventral to the internal carotid foramen and medial to the piece of bone Baskin (1981: 127) suggested might be a rostral entotympanic, a small foramen in the right position and orientation to be the posterior opening of this canal. There is no visible sulcus leading in any direction away from this foramen, however, and no clear suggestion of what it may have conveyed.

In those specimens missing most of the bulla, the only parts typically retained are the posterior crus of the tympanic ring and frequently the anterior crus as

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well. The medial (entotympanic?) portion of the bulla is apparently extensively co-ossified to the excccipital and mastoid, so that it is difficult to tell from the outside where the limits of the tymparic cavity are, or, in broken specimens, how much (ento)tympanic remains. Medially, if the bulla is missing, a smooth shelf of basicccipital shows the extent to which the bulla overlaps that element, but presents no evidence of stronger attachment for most of its extent. At the posterior corner, right next to the emargination for the posterior lacerate foramen, there is a small patch of roughened bone as if a firmer connection was made. Anteriorly, the surface of contact with the basisphenoid is very roughened, showing clearly the area of attachment (and the lack of any passage or channel, as mentioned just previously).

If the medial half of the fully ossified bulla in Barbourofelis is considered entotympanic, it is very important to note that not only would this element differ from the entotympanic in Nimravus, Dinictis, and Hoplophoneus in being thoroughly co-ossified with the ectotympanic and thus forming a fully ossified bulla, but it would also differ in being clearly unilaminar, indistinguishable from the medial walls of any other, very inflated, carnivoran bulla. In those specimens in which a complete bulla is not present, the condition is clearly due to breakage; there is nc good evidence of variation in

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completeness of ossification within Barbourofelis.

Tympanic Roof

Contrary to the first impressions of depth, generated by the very long mastoid and postglenoid processes forming tall lateral margins to the auditory region, the promontorium is actually very shallowly placed when compared to the level of the basioccipital. As can be clearly seen in UF 36867, the promontoria are in approximately the same plane as the basioccipital. The basisphenoid may be a little more ventrally situated, but not much.

Petrosal.--The almost conical promontorium is flanked on every side except laterally by a broad, gently sloping shelf that overlies the inturned dorsal lip of the (ento?)tympanic. There is no sharp demarcation by a ridge or change in slope to indicate the position of the edge of the bulla as one typically sees in other carnivorans: the edge of the bulla is attenuated and has an irregular margin (see Figure 40). But the extent of overlap seems to be clearly indicated nonetheless in some specimens by a slight change in the texture of the surface, and in UF 36867, by a sharp change in color of the petrified bone.

There are no grooves across the ventral surface of the promontorium in any of the specimens examined here.

A large, shallow, ventrally facing concavity marks

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the aperture of the cochlear fossula--markedly larger than the apertures in the other three genera studied here in detail. It is variable to what extent the rim of this fossula, especially the medial side, may be shallowly emarginate. In no specimen examined here, however, was there a distinct channel or sulcus running to or crossing the aperture of the fossula.

The smaller, oval vestibular fenestra is positioned as in the other nimravids--dorsally on the anterolateral face of the promontorium.

Because of the great height of the lateral wall of the auditory region and the completeness of the co-ossification between the tegmen tympani and the squamosal, it is generally difficult to see the facial foramen or the condition of the facial sulcus. This area is usually inaccessible in intact specimens and is broken in isolated petrosals. In UF 36867, however, most of the tympanic ring is missing and a short facial sulcus can be seen between the base of the facial canal along the medial face of the mastoid and the facial foramen in a typical position immediately anterolateral to the fenestra vestibuli. A small circular opening into the facial canal within the petrosal is visible medially, in the posterior margin of the fossa muscularis major, but this appears to be a small imperfection compared with the much more open channels often seen in the other nimravids.

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The fossa muscularis major is a shallow depression anterior to the promontorium, partly contained on the medial edge of the tegmen tympani and partly on the epitympanic wing from the anterior margin, of either squamosal or sphenoid or both. There is no anterior, epitympanic wing from the petrosal.

Laterally, the epitympanic recess is a large, hemispherical concavity, partly bounded by the lateral edge of the tegmen tympani, but largely contained within the squamosal. The suture between the two portions is visible on the right side of UF 36867. A tiny, apparently anteriorly directed foramen is present in the posterior wall of the epitympanic recess, immediately adjacent to the facial sulcus.

Sphenoid.--The main part of the tympanic cavity roof is formed by an epitympanic wing from the alisphenoid: both UF 36867 and F:AM 61895 exhibit a suture between the alisphenoid and squamosal anterior to the cavity, which can tentatively be traced posteriorly in UF 36867 to the center of the fossa muscularis major. In this latter specimen, a small slitlike foramen is present anterior to the fossa.

Farther anteriorly and ventrally, the anterior wall of the tympanic cavity is grooved by two or three clear channels, forming two or more foramina in the Glaserian fissure when the tympanic is in place, as in UF 24432 or

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F:AM 61871.

Medially, an epitympanic wing of the basisphenoid completes the roof, bearing on its ventral surface a distinct sulcus for the pterygoid nerve and medially a large rugose area to which the anteromedial corner of the bulla attaches.

Squamosal.--As mentioned earlier, the squamosal laterally provides most of the wall of the epitympanic recess. The anterior crus of the ectotympanic must be co-ossified with the squamosal because at least a fragment always remains attached to the base of the glenoid pedestal. Similarly, the posterior crus is also co-ossified with the squamosal or mastoid just anterior to the hyoid process. There is no hint of a suprameatal fossa above the osseous external auditory meatal tube.

Principal Tympanic Spaces and Foramina

For the size of the skull in Barbourofelis, and compared with the other nimravids, the total volume of the hypotympanic sinus is large, and the bulla remarkably inflated. In addition to the swollen medial and ventral walls, the bulla is inflated into the large mastoid process. The size of the mastoid sinus varies, but in some (e.g. UF 23796) is not only large but the aperture to the sinus may even be slightly restricted, so a distinct chamber is formed.

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Tympanic cavity.--Compared with the large hypotympanic sinus, the tympanic cavity proper is rather narrow and small. The roof is only slightly recessed, and the fossa muscularis major shallow.

Epitympanic recess.--The epitympanic recess constitutes the largest part of the tympanic cavity, being excavated into the squamosal dorsal to the rim of the tympanic annulus. It is a simple hemispherical concavity, without the subsidiary deeper pocket noted in the other three forms. A small foramen in present in the posterior wall of the recess in UF 36867, but none is apparent in F:AM 61961. In the latter, a tongue of ectotympanic, from the posterior rather than anterior crus, extends dorsally into the lateral wall of the epitympanic recess, next to the facial sulcus.

Posterior lacerate foramen and adjacent foramen.--A large confluence encompasses both the posterior lacerate and hypoglossal foramina. Within this, only one foramen provides exit for both sigmoid and inferior petrosal venous sinuses as well as nerves IX, X, and XI. There is no separate petrobasilar foramen as there is in the other nimravids. The common posterior lacerate foramen varies in size and position. Some are very large, open gaps at the posteromedial corner of the bulla (e.g., F:AM 61876), while others are smaller and more laterally placed (e.g., F:AM 61871). Several specimens are broken in ways that

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enable one to see the open sulcus on each side of the basioccipital for the inferior petrosal sinus. In F:AM 61895, these sulci are rather diagonally placed, fairly deep, and very well defined, and can be seen to run directly to the posterior lacerate foramen at the posterior end of the bulla.

Internal carotid foramen.--UF 24432 is an isolated temporal region with the petrosal in place and the epitympanic wing from the alisphenoid intact. It thus shows very well the interal carotid foramen, bounded anterolaterally by alisphenoid, anteromedially by the anteromedial extension of the bulla, and posteriorly by the petrosal. A sulcus in the alisphenoid margin is directed anteriorly out of this foramen. As mentioned above, this foramen is rather large compared to the size of the vessel implied by the foramen in the posterior wall of the bulla, but no grooves or sulci are present to give clues about other good-sized vessels that may have joined the internal carotid artery.

Posterior carotid foramen.--Barbourofelis differs from the other paleofelid genera in having a rather more medially placed posterior carotid foramen, ventral to the large posterior lacerate foramen rather than far lateral to it. Furthermore, instead of being a simple foramen through the wall of the bulla, or even a short canal through a thick bilaminar entotympanic, the canal here

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most reasonably interpreted as being that of the internal carotid artery appears to be formed by a fold of the tympanic in F:AM 61876 and 61871, and fully within the crista of UF 24432. (The internal structure of F:AM 61895 is not visible, but the external position of the foramen is comparable to that of UF 24432.) Internally, the canal thus enclosed by the tympanic bone runs anterolaterally to the promontorium, opening onto the promontorium immediately medial to the cochlear fossula, thus tracing a path like that of the so-called "promontory artery" or "promontory branch of the internal carotid artery". The posterior carotid foramen is frequently accompanied by at least one other foramen or channel in the fold of bulla, presumably for the internal carotid nerve.

Other foramina and fenestrae.--A distinct sulcus for the nerve of the pterygoid canal is usually visible on the ventral surface of the sphenoid, ending anteriorly at the entrance to the pterygoid canal. Posteriorly, the sulcus usually weakens, but in UF 36867, a foramen is visible in line with the sulcus, at the anteromedial corner of the fossa muscularis major, between the tegmen tympani of the petrosal and the epitympanic wing of the alisphenoid. On the cranial side, the dorsal end of this passage lies just lateral to the internal carotid foramen, at the level of the hiatus facialis in the face of the petrosal.

As noted for the other nimravids, the foramen ovale

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is sunk into a common fossa with the posterior alar foramen, although not as deeply as typical for the others.

The Glaserian fissure is frequently formed into one or two distinct foramina, presumably for passage of the chorda tympani nerve and associated blood vessels out of the tympanic region between the ectotympanic and sphenoid or squamosal.

Lateral to the Glaserian fissure is the postglenoid process and tympanic notch. In Barbourofelis, there is no trace of a postglenoid foramen, implying that the rather large sigmoid sulcus must have carried the entire venous drainage from the transverse sinus intracranially, transmitting it to the internal jugular via the posterior lacerate foramen.

Continuing laterally and posteriorly, we come next to the position of the stylomastoid foramen. What is visible next to the bulla, however, appears to be a confluence of the vagina processus hyoideus and the foramen stylomastoideum definitivum. This deep pit may be large and moderately pinched in the center (e.g. F:AM 61895) or may be a simple circular aperture (e.g. F:AM 61871, Figure 40).

In UF 24432, the bony canal flooring the path of the auricular ramus of the vagus nerve has broken open. This enables one to trace with ease the path of the large ramus from the dorsal-most foramen in the common posterior

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lacerate foramen, at the level of the posterior edge of the petrosal, towards the facial canal on the medial face of the mastoid.

A last, puzzling foramen may be mentioned here. On the ridge of exoccipital forming the lateral margin of the posterior lacerate foramen, there is in UF 24432 a moderately sized foramen, apparently headed anterolaterally into the exoccipital towards the mastoid. That it gave passage to any vessel or nerve is perhaps doubtful: most of the bone in the skull of Barbourofelis is so cancellous as to be almost frothy, and this hole could easily be just a cell at the surface in a spot where the periosteum failed to cover it.

Adjacent Cranial Morphology

Basisphenoid.--Unlike the other nimravids, Barbourofelis has a bulla with an anteromedial process projecting beneath the basisphenoid, which is relatively flat with rugose concavities to receive the process on each side. Thus the sloping shape is much the same, but here is composed of tympanic rather than basisphenoid. The exposed ventral surface of the basisphenoid is very narrow between the anteromedial processes.

Basioccipital.--Similarly, only a narrow strip of basioccipital is exposed anteriorly between the inflated bullae. Rather than being troughlike, however, as was the

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case in Hoplophoneus for example, the basioccipital in Barbourofelis has a sharp ridge down the midline (higher and extending farther forward than that seen in Hoplophoneus), and very low ridges on each side at the edge of the exposed ventral surfaces. Further laterally, the basioccipital overlies the bullae in a broad flat shelf that bears on its dorsal surface an open channel for the inferior petrosal sinus. Thus, there is no development of the deep vertical flanges seen in other nimravids, but rather a broad, horizontal contact, little if any recessing of the auditory region above the level of the basioccipital, and no flange roofing the sulcus for the inferior petrosal sinus.

Lateral margin of auditory region.--Obviously correlated with the extreme sabertoothy in these animals, the glenoid fossa is set on the end of a large, ventrally directed pedestal, forming the anterior side of the deep tympanic notch. Similarly, the mastoid process is huge, forming the posterior wall of the notch. More variation in the orientation of the blunt end of the mastoid process is evident within Barbourofelis than was the case in Hoplophoneus, but in general, it faces more directly ventrally. The tympanic notch is roofed by a moderately wide, lateral shelf of squamosal, certainly never as extreme as that observed in the largest Hoplophoneus (F:AM 102387).

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Because of the great degree of co-ossification, it is not possible to distinguish a processus hyoideus from the mastoid. In a couple of specimens (e.g. UF 36867), it appears as if the hyoid apparatus might attach at a point posterior to the stylomastoid foramen, but this is certainly not clear. Although the suture can only be tentatively traced, the condition in the juvenile B. morrisi and the more complete B. lovei specimens is that the mastoid process is constituted entirely of mastoid, with only a very small contribution of squamosal at the base anteriorly.

Paroccipital processes are entirely absent, apparently replaced functionally by the broad posterior expanse of the mastoid processes, as indicated by the rugose areas to each side of the occipital condyles.

Intracranial Morphology

Petrosal.--Two isolated petrosals, as well as a variety of skulls broken so that the intracranial structures are visible, permit description of the cerebellar face of the petrosal and surrounding structures. In general outline, the petrosal intracranially is a long, low triangle. There is a distinct, flat anterolateral face that lies appressed to the broad tentorium osseum. The dorsal half of the crista petrosa is sharp, dividing this anterolateral face from

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the cerebellar face, although it does not continue ventrally to the rostral apex, nor is it produced into the large flange such as is found in canids. Anteriorly, the rostral apex is long, extending forward to the basisphenoid.

Posteriorly, the petrosal presents a wide face behind the internal acoustic meatus, contributing a little to a very broad, poorly defined sigmoid sulcus. Dorsally, this broad face is concave, forming a shallow subarcuate fossa. A long face of the pars mastoidea protrudes dorsally, paralleling the very vertical lambdoidal crest. This process extends diagonally across the sigmoid sulcus in UF 24432, but in F:AM 61961, although broader, appears to be entirely anterior to the sulcus.

The internal acoustic meatus is irregular (and variable) in outline and the separation of the facial and vestibulocochlear canals is deep within the meatus. (The dorsal passage is not subdivided in either UF 23796 or F:AM 61895, whereas the ventral canal is divided in half by a bony partition in both.) Not only is there no appearance of swelling around the internal meatus (as there is in Hoplophoneus), but the whole cerebellar face of the petrosal is either flat or shallowly concave.

Deep slits and crevasses run along the medial edge of the petrosal, giving it a jagged, layered appearance. In none of the specimens I have examined has the petrosal

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actually abutted the basioccipital. Only in one, the petrosal from UF 23796, is there any kind of smooth area along this medial edge, and in that specimen only anteriorly. The inferior petrosal sulcus on the basioccipital is broad and does not appear to typically involve the petrosal.

The aperture of the osseous canal for the vestibular aqueduct may be tentatively recognized on the posterior margin of the petrosal in UF 24432 and F:AM 61961, at the level of the subarcuate fossa. No aperture for the cochlear aqueduct can be identified with any assurance, because of the many slits and crevasses along the posterior and medial margins.

Intracranial canals.--The complete absence of a postglenoid foramen argues that a superior petrosal sinus was absent, and that venous drainage was entirely via the sinus in the broad sigmoid sulcus. A cross section of the canal for part of the venous drainage is visible on the left side of F:AM 61961 (Figure 42). Much of the venous system appears to have been in shallow sulci rather than enclosed in bone: a channel immediately beneath the tentorium looks as if it contributed to the sigmoid sinus.

I have not been able to recognize a mastoid foramen such as is found between the posterior wall of the sigmoid sulcus and the back of the skull in the other nimravids. A small foramen leads from the ventral end of the sulcus

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through a small, completely enclosed canal for the occipital sinus in some specimens (e.g., UF 24432, F:AM 61895, and UF 23796), but not in others (e.g., F:AM 61961, Figured in 42, and UF 36867).

Barbourofelis is also variable in possessing any foramina that can be identified as postparietal foramina. When present, they appear rather ventrally placed, because of the very pronounced sagittal crest.

No channel can be recognized for an anastomotic branch from the internal maxillary artery to the middle meningeal artery.

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MORPHOLOGICAL DESCRIPTION: FELIDAE

Since the nimravids have been thought tc be felids or closely related to felids by so many paleontologists, and since the morphology of Felis catus is one of the best known among the Mammalia, brief descriptions are provided here of the extant genus Felis, the Miocene felid Pseudaelurus (not sabertoothed at all), and the Pleistocene sabertoothed "tiger" Smilodon. These descriptions will provide a starting point for the comparison of nimravids with other carnivorans, thereby including another sabertoothed carnivoran.

FELIS

Based in detail on a series of 15 uncatalogued Felis catus, sectioned in a variety of planes, and AMDM 175101, Felis rufus.

Tympanic Floor: Auditory Bulla

The ectotympanic is a dense bone enclosing the anterolateral chamber in the felid bulla. The crura appear to meet above the external auditory meatus, although at this point they are thoroughly co-ossified with the squamosal. An irregular oval meatus is formed by the thickened margin, facing slightly anterior as well as laterally, but well behind the postglenoid process; the

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meatus is in no way obstructed by the postglenoid process as was observed in nimravids.

A hooklike processus tubarius projects medially from the broadened anterior crus, sticking out horizontally beneath the anterior portion of the fossa muscularis major. The tip of the process turns anteromedially towards the canalis musculotubarius. Anterior and medial to this process, the anterior crus expands into a broad, cuplike shape encompassing a larger chamber internally than would be deduced from the ventral suture of the septum.

No external meatal tube is present, but the thickened rim of ectotympanic around the meatus is wider anteriorly so that the crista tympanica and tympanic sulcus are set at a slightly more oblique angle than the external meatus. This angle is a little greater than 30 degrees, both from a line directly anterior-posterior, and also from the vertical.

The narrower posterior crus of the ectotympanic is fused to the anteromedial corner of the mastoid, next to the hyoid process and anterior to the facial canal. Ventrally, the ectotympanic is expanded, its medial extension curving around to abut the entotympanic and form the dorsally directed septum.

A styliform process is very rarely identifiable on F. catus; often the anteromedial process is misidentified as

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a styliform process. The specimen of F. rufus studied, however, had distinct styliform processes projecting anteromedially beneath the canalis musculotubarius, with a dorsal ridge partially subdividing that passage.

A very thin-walled, inflated entotympanic forms the rest of the bulla, enclosing a second chamber partially medial but mostly posterior to the tympanic cavity proper. As can be seen in a frontal section through the bulla, the dorsal rim of the septum traces a curve, first directed posteriorly from the anterior corner, then bending beneath the promontorium to run laterally, directly below the aperture of the cochlear fossula, toward the stylomastoid foramen.

Low crista or partial septa are occasionally found projecting from the entotympanic walls in Felis, but not large ones, nor are they found with any regularity of position. The internal carotid artery is so reduced in F. catus that no channel for it can be easily found. Long anteromedial processes project forward from the entotympanic portion of the bulla, lying appressed to the basisphenoid. Occasionally, the basisphenoid also produces flanges next to these processes (Figure 43), but this is rare and never replaces the anteromedial processes entirely.

Tympanic Roof

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As in Barbourofelis, the medial side of the roof of the auditory region in Felis in not recessed above the level of the basioccipital. Usually the promontoria are on the same level as the midline bones, and occasionally will even project slightly ventral to the basioccipital (as in skull number 16 in the AMNH teaching collection). Laterally, the roof of the tympanic cavity proper, the fossa muscularis major and epitympanic recess, are set much more dorsally.

The rounded, almost bulbous promontorium constitutes a much larger amount of the ventral surface of the petrosal in Felis than in the nimravids. Entotympanic overlaps the edges of the basioccipital as well as the skirts of the promontorium. All surrounding elements contact the petrosal closely; the rostral apex of the petrosal even overlies the epitympanic wing of the sphenoid.

On the ventral surface, the aperture of the cochlear fossula is usually quite round, of a moderate size, and directed both posterolaterally and ventrally. Dorsally on the anterior side of the promontorium, the vestibular fenestra is small and very round, and appears to be set inside a shallow fossula, the dorsal rim of which is the posterior margin of the facial canal. No grooves were noticed on the ventral surface of the petrosal.

The facial foramen is positioned very far laterally,

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and above a strut of bone extending from the lateral margin of the fossa muscularis major to a broad contact below the processus hyoideus (see Figure 43). Turning posteriorly almost immediately, the facial sulcus runs to the base of the mastoid process and ventrally down its medial face, covered over medially by entotympanic.

A large, hemispherical fossa muscularis major is entirely contained within the tegmen tympani of the petrosal. Laterally, the medial third of the epitympanic recess is roofed by the petrosal, and the rest by the squamosal. In some specimens, I think I can see what may be a small foramen in the posterior part of the epitympanic recess, but not with any certainty. And certainly Davis and Story (1943) did not show the passage of any nerve or artery at that point.

Medial to the fossa muscularis major, the petrosal is emarginate, matching a deeper notch in the epitympanic wing of the sphenoid, for the passage of the greater superficial petrosal nerve extracranially towards the pterygoid canal, through a distinct groove on the ventral surface of the sphenoid.

Principal Tympanic Spaces and Foramina

A large hypotympanic sinus and tympanic cavity proper are enclosed by the inflated bulla. Expansion posteriorly, behind the petrosal, results in an excavation

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into the paroccipital process, so that the latter cups the rear of the bulla.

Much has been made by some of the inclusion of the hypoglossal foramen in a common fossa with the posterior lacerate foramen in felids or aeluroids. As demonstrated by Clark and Guensburg (1972), this condition is variable, not only within the family Felidae, but within species. When confluence is present, it is a function of both the anterior direction of the opening of the hypoglossal foramen and the presence of ridges, one running back from above the medial margin of the bulla, and the other transversely from the paroccipital process. Although variable, confluence is apparently a derived feature within the Aeluroidea.

A single foramen at the posteromedial corner of the bulla, the posterior lacerate foramen, provides egress for the three cranial nerves IX, X, XI and the two venous sinuses, the inferior petrosal and the sigmoid, often already confluent as the internal jugular vein. This large foramen is quite medially placed.

An internal carotid foramen is present, just anterior to the rostral apex of the petrosal, in a deep notch in the basisphenoid. Although Davis and Story (1943) demonstrated that the internal carotid in the domestic cat is occluded at the level of the bulla, they found instead that an anastomotic branch from the ascending pharyngeal

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artery passed posteriorly into the aperture at the anteromedial corner of the bulla, next to the canalis musculotubarius proper, joined the loop of interal carotid artery and thus formed part of the cerebral arterial supply. When a posterior carotid foramen can be identified in Felis, it is a small foramen entering the bulla or a passage between the bulla and the basioccipital at the anterior-most corner of the posterior lacerate foramen.

An alisphenoid canal is entirely lacking; the foramen ovale is in a fairly typical position medial to the glenoid fossa. The passages for the chorda tympani nerve and associated blood vessels are small, distinct foramina within the Glaserian fissure. Modern felids are usually said to be lacking postglenoid foramina. Certainly they are extremely small, but several of the Felis skulls I examined had very tiny, bilateral foramina on the posterior wall of the postglenoid process.

A tiny canal between the exoccipital and mastoid posteriorly and the entotympanic anteriorly gives passage laterally to the auricular ramus of the vagus nerve, from the posterior lacerate to the facial canal.

Adjacent Cranial Morphology

Both basisphenoid and basioccipital are broad and relatively featureless ventrally. Lateral to the auditory

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cavity, the glenoid fossa is transversely elongate, as is common among carnivorans, and not pedestalled. The tympanic notch is shallow, overhung by a moderately broad, slightly concave, squamosal shelf. Within domestic cats, the size of the mastoid process is rather variable. In the wild species, the mastoid is usually of moderate size, but certainly nothing like the hypertrophied processes of nimravids. The paroccipital processes are broad, thin sheets of bone appressed to and cupping the posterior part of the bulla. Projecting paraoccipital processes may be more or less developed within felids, in addition to these cupping sheets of bone.

Intracranial Morphology

The petrosal presents a rather triangular or pointed oval shape intracranially. A broad anterolateral face is overlain by a well developed tentorium; the crista petrosa is sharp dorsally, much as in Barbourofelis. The subarcuate fossa is distinct and rather deep in these specimens, the rounded prominence of the superior or dorsal semicircular canal often showing clearly around the fossa. The internal acoustic meatus is a single deep opening.

A shallow emargination across the rostral apex may represent a sulcus for the trigeminal nerve, but this is not clear. The hiatus facialis opens on the anterolateral

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face, usually covered by the tentorium. A fissure-like opening at the tip of the rostral apex is the intracranial aperture of the internal carotid foramen. One of the several tiny foramina in the margin of the petrosal dorsal to the posterior lacerate foramen must represent the aperture of the bony canal for the cochlear aqueduct. More dorsally, the opening of the canal for the vestibular aqueduct and the slit that housed the endolymphatic sac is evident.

Most of the venous drainage from the posterior portion of the braincase and meninges collects in the sigmoid sinus, lying in the broad sulcus posterior to the petrosal (Figure 44), and exits the skull via the posterior lacerate foramen. Ventrally, the petrobasilar canal, formed by the medial margin of the petrosal and the sulcus in the basioccipital, houses the inferior petrosal sinus, connecting the cavernous sinus anteriorly and the internal jugular posteriorly.

The canal in the exoccipital for the occipital sinus runs from the posterior margin of the sigmoid sulcus back to a lateral foramen at the posterior margin of the walls of the foramen magnum. I can not find any more dorsal exit from the sigmoid sulcus to a mastoid foramen as seen in Dinictis, Nimravus, or Hoplophoneus, nor can I find a postparietal foramen externally. Finally, I can not find clear evidence in the intracranial surface of the bones

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for an anastomotic ramus from the internal maxillary artery to the meningeal artery.

PSEUDAELURUS

Based in detail on F:AM 61834, F:AM 61835, and F:AM 69330.

Tympanic Floor: Auditory Bulla

Complete bullae are fairly frequently preserved in fossil felids: the septum apparently strengthens the bulla, since if it is broken, often the ectotympanic with septum will be the main structure remaining. Somewhat as in Felis, the ectotympanic is an inflated, shieldlike structure enclosing an anterolateral chamber below the tympanic cavity proper. The external auditory meatus faces roughly anterolaterally, but again is entirely posterior and well removed from the postglenoid process. Rather than presenting an appearance of "tucked in" dorsal margins, the front margin of the ectotympanic is splayed out, forming skirts that lap up on the posterior face of the squamosal and sphenoid in front of the bulla. Thus the anterior crus is very broad, with a large area of attachment to the anterior margin of the auditory region.

Faint sutures may be made out in F:AM 61835, indicating that the crura of the ectotympanic do not meet

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dorsally, so that the dorsal portion of the tympanic notch is squamosal. The posterior crus is also broad, and extensively fused to the mastoid and hyoid processes. Inside the ectotympanic, the plane of the crista tympanica makes horizontal and vertical angles of about 30 degrees with the sagittal plane. Dorsal to the meatus, a broad processus tubarius projecting medially from the anterior crus is visible through a break in the septum.

The septum is oriented diagonally, as in Felis, immediately ventral to the highest point of the promontorium and laterally, directly below the aperture of the cochlear fossula, to terminate in the medial wall of the vagina processus hyoideus. The anterior end of the septum between the chambers reaches the medial wall of the bulla, posterior to the anteromedial process so that the latter appears to be entirely ectotympanic in Pseudaelurus. Anteriorly, the aperture of the canalis musculotubarius is low, with a distinct sulcus on its ventromedial margin, as if for a medium-sized vessel entering the canal from a posteroventral direction. There is no styliform process present.

A large posteromedial chamber is formed by the inflated, thin-walled entotympanic. As in modern felids, the hypotympanic sinus extends well posterior to the petrosal. The internal surface of the entotympanic may be either smooth (F:AM 61835) or have small partial crista

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(F:AM 69330). A small foramen at the anterior-most end of the posterior lacerate foramen appears to represent the posterior aperture of a canal in the entotympanic or between the entotympanic and the basioccipital for the internal carotid artery and thus may be identified as the posterior carotid foramen.

Tympanic Roof

As in Felis, the auditory region as a whole is only moderately excavated, so that the promontoria are either on the same plane as the basioccipital (F:AM 69330) or slightly above that plane (F:AM 61835). No auditory region is missing enough of the bulla for me to be able to see clearly the relationships between the petrosal and the surrounding elements. The roof of the tympanic cavity can not even be seen except through a break in the septum. The aperture of the cochlear fossula is small and round, facing posterolaterally and not particularly ventrally. There are no grooves evident on the small area of petrosal exposed.

Principal Tympanic Spaces and Foramina

An initial examination suggests that the posterior entotympanic cavity is by far the largest, but re-evaluation reveals that the tympanic cavity proper, above the ectotympanic, is fairly deeply incised into the

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bottom of the skull, much as is seen in Felis (see Figure 47). The anterior chamber is not particularly inflated ventral to the crista tympanica, however.

A "typical aelurbid" condition is seen in the apparent confluence of the hypoglossal and posterior lacerate foramina. However, this confluence is due mainly to a very strong ridge behind the foramina from the paroccipital processes. The ridge anteriorly to the medial side of the bulla is poorly developed compared to the condition in Felis, largely because the hypoglossal foramen is so medially placed. The posterior lacerate foramen is itself very medially placed, and evidently transmitted both venous sinuses as well as the three cranial nerves--there is no separation of any foramen to the petrobasilar sulcus.

Dissection and further preparation of the skulls would be required to determine the size and position of the internal carotid foramen. A moderately large one is predicted by the identification of the sulcus in the ventral lip of the canalis musculotubarius as being for a large anastomotic branch from the ascending pharyngeal artery. Thus examination of the internal carotid foramen will serve as as test of that hypothesis. Similarly, other foramina in the squamopetrosal or sphenopetrosal suture can not be determined from the material at hand, but the presence of one for passage of the greater

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superficial petrosal nerve to the ventral surface of the sphenoid is predicted by the identification of the groove leading to the pterygoid canal as that for a typical pterygoid nerve.

Among the other foramina to be mentioned, there is the foramen ovale: the alisphenoid canal is variably complete (but at least partially indicated in all three specimens), and shows a similar variation in whether or not its posterior (alar) opening is set in a common fossa with the foramen ovale. In F:AM 61834, the canal is complete, and there is a common fossa of about the depth seen in Canis. At the other extreme, F:AM 61835 has bony flanges that do not meet to form a canal (but this may be due to postmortem damage). The partial posterior alar foramen that is thus traced is separate from the foramen ovale; the dividing bar of bone is on the same level as the surrounding bone.

Only very small, bilaterally asymmetric foramina can be seen in the Glaserian fissure. No postglenoid foramina can be seen in any of the three specimens examined here. The stylomastoid foramen is bounded laterally by the mastoid and medially by the entotympanic, and is positioned immediately posterolaterally to the vagina processus hyoideus within the ectotympanic.

Adjacent Cranial Morphology

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Both basisphenoid and basioccipital are moderately broad and relatively unsculptured, except for rugosities posteriorly on the latter for the insertion of the longus capitis and rectus capitis ventralis muscles. Sulci for the pterygoid nerves are evident on the ventral surface of the basisphenoid. Anteromedial processes from the bullae are present, but are short compared to those of modern felids. The basisphenoid is produced into low flanges and partial buttresses anteriorly, not nearly as extreme as in nimravids, but typically a condition seen infrequently in modern felids.

The glenoid fossae are transversely elongate, as is typical for carnivorans, and project laterally from the skull, without any ventral pedestalling. Medially, a ridge continues from the postglenoid process, so that the anterior margin of the auditory region is a more vertical wall than is usually seen in front of a region not deeply excavated.

These three skulls are moderately large (puma to leopard size), and therefore have moderately sized mastoid processes, not particularly ventrally produced, but somewhat enlarged laterally at the base of the lambdoid crest (Figure 45). The mastoid process is formed entirely of the pars mastoideus, but the anterior surface and edge of the crest at the posterior side of the tympanic notch is squamosal. A crest joins the mastoid and paroccipital

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processes, but is not widened at any point into a shelf. The exoccipital forms a pendulous sheet that cups the back of the bulla; the tip of this paroccipital process may variably form a more projecting process. (Such variation is seen in modern felids as well, and in extreme cases does not differ much from the canid condition. In canids, however, the mastoid is greatly reduced, and the connecting ridge lost.)

Intracranial Morphology

Some of the internal features can be seen in F:AM 61835. A large, well ossified tentorium obscures much of the area of interest, however. The petrosal is rather rounded, without a sharp rostral apex. A distinct subarcuate fossa is present dorsally. The triangular internal acoustic meatus is more shallowly subdivided than was seen in nimravids, but no more so than is sometimes seen as a variant in modern felids. The position of the aperture of the cochlear aqueduct can not be determined with certainty, but a slit on the posterior margin at the level of the internal acoustic meatus can be identified as the slit for the endolymphatic sac.

The lack of a postglenoid foramen would predict the absence of a superior petrosal sinus, and suggest that the venous drainage was via the sinus in the sigmoid sulcus. The latter is only of moderate size but is deeply incised

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into the cranial bones, and is confluent ventrally with a very large and deeply incised sulcus for the inferior petrosal sinus. The medial margin of the petrosal does not appear involved at all in this sulcus, which channels deeply into the lateral margins of the basioccipital and is almost completely open dorsally. A posterior opening of a canal for an occipital sinus can be seen on each internal wall of the foramen magnum; the anterior opening is presumed to lie in the posterior wall of the sigmoid sulcus. A foramen in the correct position to be a mastoid foramen is present on one side but not on the other; the presence of a corresponding foramen in the wall of the sigmoid sulcus could not be determined.

SMILODON

Based in detail on LACM HC 6997 (sectioned left ear region; figured in Merriam and Stock, 1932, Plate 15, Figure 1), LACM HC 6998, LACM HC 6999, LACM HC 7000, LACM HC 7001.

Because Merriam and Stock (1932) so thoroughly described and illustrated the whole skull of Smilodon, my description will be abbreviated, and depend on theirs, especially for the description of the surrounding features. Some comment, however, is needed as context for

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some of the points in which I disagree with Hough's (1953) analysis of Smilodon's auditory region.

Tympanic Floor: Auditory Bulla

Because of the enlargement of the mastoid processes and pedestalling of the glenoid fossae, the tympanic notch is tall and narrow, as in the sabertoothed nimravids. Merriam and Stock (1932: 33) were correct that the tubular form of the external auditory meatus (fitting into that long, narrow notch) is unlike the non-sabertcothed felids, but failed to mention the equally significant point that it is also very different from the condition in nimravids. The meatus itself is no wider than the notch, and is directed straight through the notch. The ectotympanic is widened, and is not the diagonal plate seen in even the sabertoothed forms, such as Hoplophoneus and Eusmilus. The crura of the ectotympanic in Smilodon are so thoroughly co-ossified with the squamosal that one cannot establish with certainty whether the ectotympanic forms a complete circle as it appears to, or whether the squamosal is overhung and ridged dorsally, creating that appearance. The shortness of the anterior crus in the juvenile, LACM HC 7000, argues for the latter.

The canalis musculotubarius appears to be formed entirely in ectotympanic (seen in cross section LACM HC 6997). Its ventral edge bears a small styliform process

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in front of a fairly large rugose area on the bulla. Anteromedial processes are present, formed by the bulla, but by which element is unclear. One or more puzzling foramina are present on or near the anteromedial process, and will be considered later.

Internally, the crista tympanica and tympanic sulcus slope at an angle of nearly 30 degrees from vertical, but around an axis directed almost exactly anteroposteriorly, all in direct contrast to the condition in nimravids.

Merriam and Stock described the septum exactly as it appears to me. It matches the septum in non-sabertoothed felids in a variety of respects: its vertical orientation, its curled, thickened edge, its path directly below the promontorium in a broad curve, passing directly beneath the most prominent part of the promontorium, and bulging so as to present a convex shape to the hypotympanic sinus and a concave one to the tympanic cavity sensu stricto. My observations do not agree with Hough's (1953: 102) description of the orientation of the septum.

The sectioned specimens show clearly that the entotympanic was a single layer, solid bone, and relatively thin although encompassing a chamber of fairly large volume. In none of the specimens I examined was the secondary crista as large as implied by the description in Merriam and Stock (1932: 33-34). All specimens matched

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the one illustrated by them in their plate 15 in that the excavation into the mastoid formed in cross section a circular shape of a different radius, so that the total cross section was more pear shaped than circular in outline, with low crista at the indentations, marking (as Merriam and Stock pointed out) the inner limit of the mastoid.

Tympanic Roof

Although the elongate mastoid processes and glenoid pedestals give an impression of depth, as in Barbourofelis, when the level of the petrosals are compared to the plane of the basioccipital, one finds that, in Smilodon, the petrosals are only slightly recessed above the level of the basioccipital, and the roof anterolateral to the petrosal not much further than that.

The aperture of the cochlear fossula is round, medium-sized, and directed rather ventrally as well as posterolaterally. The fenestra vestibuli is oval and faces anterolaterally. There is one very faint suggestion of a groove on the ventral surface of the petrosal, in section "C" of LACM HC 6997 (labelled in Merriam and Stock's Plate 15): a narrow shiny trail heads anteromedially from the posterior (cut) margin between the aperture of the cochlear fossula and the inturned edge of

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the bulla, towards that bullar edge, disappearing beneath it just posterior to the septum. Judging from section "D", this groove appears to be a continuation of the deeply incised channel, in the roof of the posterior part of the bulla, that I interpret as having housed the very reduced internal carotid artery or nerve or both.

The facial foramen opens immediately dorsal and lateral to the vestibular fenestra, from which point the sulcus heads posteriorly to the base of the facial canal, then dives ventrally between the bulla and the mastoid to exit via the stylomastoid foramen. In LACM HC 6997 (the only specimen in which this part of the petrosal is both relatively complete and visible), there is a fenestra in the wall between the intrapetrosal facial canal and the fossa muscularis major, but this appears to be a break.

Both the fossa muscularis major and the epitympanic recess are in their usual positions, but both seem a little small and shallow for the size of the region, although this may again be a misleading impression generated by the huge mastoid processes. Whether these recesses are totally roofed by petrosal, or how much is contributed by epitympanic wings from the sphenoid or squamosal, can not be determined from the sectioned specimens since they are all adults with well closed sutures. A foramen passes anteriorly, apparently out of the epitympanic recess, but I suspect this is for the

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passage of the chorda tympani nerve over the ectotympanic and out the Glaserian fissure between ectotympanic and sphenoid. Certainly a foramen is present externally at the proper spot for its exit. There is no secondary recess in the epitympanic recess.

Principal Tympanic Spaces and Foramina

The hypotympanic sinus is actually quite large, extending in a large excavation into the mastoid processes, and enlarged far posterior to the petrosal. (It is perhaps this posterior enlargement that Hough (1953: 102) meant when she said that the sinus "continues into the paroccipital". At least in LACM HC 6997, however, the sinus does not extend past the level of the transverse ridge connecting hypoglossal and posterior lacerate foramina, so although it is cupped slightly by the exoccipital, the paroccipital process projects further back, and is apparently entirely cancellous bone.)

As just alluded to, the hypoglossal is set close to the posterior lacerate foramen. The latter is a large gap positioned at the posteromedial corner of the bulla. Both the wide sigmoid sulcus and the shallow, ill-defined channel for the inferior petrosal sinus run to the margins of the posterior lacerate foramen, suggesting a confluence and common exit in typical carnivoran fashion from a medially placed foramen.

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Most bulla appear to show a deeply incised, small groove or even canal that begins in the bulla in the posterior lacerate foramen and travels roughly anterolaterally to the dorsal surface of the bulla, and thence between the bulla and petrosal (see Figure 46). This is identified as a carotid canal, but I have been unable to determine to my satisfaction the anterior route of this canal, nor with certainty an internal carotid foramen (but this will be discussed below). The posterior carotid foramen would be that point where the groove becomes a completely closed canal, which may never happen on some, and on others appears to be fairly far dorsal, such as that illustrated, LACM HC 7000.

One or two foramina are visible on the ventral surface of the anteromedial bullar process or the sphenoid immediately adjacent. On the left side of LACM HC 7000, the dorsal part of the bulla is missing and one can see a rather large smooth channel in the sphenoid overlying the anteromedial process, ending in the anterior-most foramen in the sphenoid at the base of the pterygoid ridges, and running from the sphenopetrosal suture at a point just lateral to the rostral apex of the petrosal, right in line with the hiatus facialis. Probing of the foramen suggests that the passage beyond heads anteriorly inside the bone (the basisphenoid I suppose, but I can not tell where the pterygoid starts). Medial to this sulcus is another

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sulcus, starting farther back from the broken edge, beneath the position of the foramen in the anteromedial process, judging from the other side. This sulcus also runs posterodorsally along the flange, to a foramen in a notch in the basisphenoid, almost encircled by the bone. This foramen, when viewed dorsally, is at the apex of the petrosal, exactly in the expected position for an internal carotid foramen.

Since there is no other groove for the nerve of the pterygoid canal, nor can I find bilaterally symmetric foramina anteriorly that are reasonable possibilities for the posterior openings of the pterygoid canal (there is one small possibility on the left side of LACM HC 7000), I conclude that either the pterygoid nerve was very reduced or absent, or it was rather large, lay in the lateral one of these sulci, and that the foramen first described is the entrance to the pterygoid canal. I hypothesize that the second foramen admitted a ramus from the ascending pharyngeal artery that coursed through the medial sulcus to the internal carotid foramen and intracranially joined the internal carotid circulation.

As in Felis, there is no alisphenoid canal; the foramen ovale is therefore relatively isolated. A postglenoid foramen is usually absent, but LACM HC 6999 appears to have a good sized one. Preparation revealed that it was actually the common fossa for a number of very

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small channels, which may indeed haved drained a slitlike remnant of superior petrosal sinus suggested by the cross section of a canal visible above the petrosal on the cut face of that specimen. As described earlier, the stylomastoid foramen is defined by mastoid laterally and the bulla medially, positioned anterolateral to the vagina processus hyoideus, which is entirely enclosed within the bulla.

Section "C" of LACM HC 6997 shows on its posterior surface an opening from the rear into the facial sulcus at the point where it turns ventrally. This opening is the anterior part of a channel between the bulla and petrosal, and posteriorly exoccipital, that would have conveyed the auricular ramus of the vagus anterolaterally to the facial canal.

Adjacent Cranial Morphology

The morphology of the bones around the auditory region of Smilodon has been well described by Merriam and Stock (1932). I supply here a few comments on the state of features specifically noted in the preceeding descriptions of other taxa.

Instead of a buttress formed of basisphenoid cupping a rounded anteromedial corner of bulla, a distinct anteromdial process from the bulla itself is present, as in Felis. There are no vertical flanges on the margins of

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the basioccipital; instead, the edge of the median element overlaps the dorsal curve of the bulla at a low angle.

The greatly hypertrophied mastoid process presents a long sweeping curve, forming a rugose crescent extending down on each side of the bulla. This is in contrast to the square, blunt mastoid processes seen in nimravids. The vagina processus hyoideus, formed entirely by the bulla, is well posterior of the ventral end of the mastoid, rather than being anteromedial to the mastoid. From LACM HC 7000, it appears that, except for a thin anterior skin of squamosal, the rest of the process is mastoid, but this is not certain.

Intracranial Morphology

The cerebellar face of the petrosal is generally oval in outline. It is clearly divided by a low horizontal ridge immediately above the internal acoustic meatus (see Figure 46). No divisions of the latter are visible as far as preparation with a needle could reach. Dorsal to the ridge, the smoothly concave face is excavated by a deep stellate pit, presumably the subarcuate fossa. Above this pit, a crista petrosa runs from the dorsal apex to the rostral apex of the petrosal.

Identification of the hiatus facialis in the center of the anterior face was confirmed by probing the channels of a sectioned petrosal (LACM HC 6997). Several openings

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occur on the posteromedial edge of the petrosal, any of which could be an aperture for the cochlear aqueduct. On the posterior edge, there is an excavation that looks like a slit whose margins have been spread, with a foramen at the bottom of the funnel--all of which presumably housed the vestibular aqueduct and endolymphatic sac. No sulcus is identifiable for the trigeminal nerve.

As Merriam and Stock (1932: 38) noted, there is a large tentorium osseum in Smilodon. The tentorium osseum is broken in the figured specimen but is evident in others (e.g., LACM HC 6998). A vestigial canal for the superior petrosal sinus may be present, a shown by LACM HC 6999, but the bulk of the venous drainage was evidently through the sigmoid sinus, as indicated by the very large sigmoid sulcus (LACM HC 6997 "D"). In this latter specimen, there is a very small canal for an occipital sinus but no trace of a mastoid foramen.

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MORPHOLOGICAL DESCRIPTION: SUMMARY

Quite unexpectedly, I found, as evident in the above descriptions, that Barbourofelis was different from the other nimravids in a large enough number of ways that I now have difficulty characterizing the basicranial anatomy of the family Nimravidae when Barbourofelis is included. The following summaries will therefore characterize first the Nimravinae and Hoplophoninae (exemplified in this study by Dinictis, Nimravus, and Hoplophoneus primarily), then contrast the Barbourofelinae (Barbourofelis). The character states are listed in very abbreviated form; for amplification refer back to the detailed descriptions of each genus. Discussions of various aspects of these hypothesized homologies, and hypotheses for the polarity of each feature, will be presented in the next section. The character states are numbered in the first summary; these numbers are carried through subsequent discussion for easy cross reference, and label the characters in the final cladogram in Figure 58.

Summary for Nimravinae and Hoplophoninae

Tympanic Floor: Ectotympanic

1. ectotympanic flat or gently curved; edge moderately expanded ventrally
2. orientation vertical, at about 30 to 45 degrees from

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sagittal plane.

3. meatus much wider than tympanic notch, extends forward on medial side of pedestalled glenoid fossa
4. crista tympanica extends only very slightly intc tympanic cavity
5. anterior crus broadened, horizontal, nearly meets posterior crus above external auditory meatus, forming a nearly closed ring
6. posterior crus short, vertical, on anteromedial side of hyoid process
7. processus tubarius present on medial side of anterior crus
8. ventral edge finished, faceted
9. long osseous canalis musculotubarius present; ectotympanic plate usually emarginate below canal
10. styliform process usually absent
11. no septum bullae present

Tympanic Floor: Entotympanic

12. tympanic floor not fully ossified; some entotympanics with finished edges
13. sandwich construction of entctympanic: very thin outer sheets of bone with thick layer inside of cancellous bone
14. anterior edge curves laterally, then posterolaterally, to form medial wall of canalis musculotubarius (="septum" of some authors)

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15. posterior (carotid?) foramen laterally positioned, through posterior wall of bulla (not yet documented in Nimravus)
16. hypotympanic sinus never invades mastoid
17. no cristae on internal surface of bulla

Tympanic Roof

18. auditory region recessed dorsal to level of basisphenoid/basioccipital
19. grooves on ventral surface of petrosal
20. epitympanic recess with secondary deeper excavation (not seen in Eusmilus)
21. sulcus, groove, channel, or canal present in anteromedial corner of auditory region, running posterolaterally and dorsally to internal carotid foramen, presumably for anastomotic branch of the ascending pharyngeal artery
22. separate petrobasilar foramen, posteriorly placed, formed by abutment of entotympanic against basioccipital or exoccipital
23. posterior lacerate foramen laterally placed (in center of posterior edge of auditory region rather than posteromedial corner)

Adjacent Cranial Morphology

24. moderate to large postglenoid foramen present
25. mastoid processes square or rectangular in cross section, with blunt ends

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26. broad crest connecting mastoid and paroccipital processes (if latter are present and distinct)
27. paroccipital processes well posterior tc bulla, not cupping rear even to extent seen in canids
28. basisphenoid forms buttress against anteromedial corner of bulla; anteromedial process from bulla never present
29. vertical flanges from basioccipital appressed against medial side of ear region

Intracranial Morphology

30. tentorium exhibiting little cr no ossification of ventral portions
31. at least some flange of basioccipital roofing inferior petrosal sulcus; matching sulcus present on petrosal, forming petrobasilar canal
32. posterior foramen from sigmoid sulcus through cranium to (external) mastoid foramen
33. (external: postparietal foramina present)

Comparison of Barbourofelinae with other nimravids

	NIMRAVINAE & HOPLOPHONINAE	BARBOUROFELINAE
4.	crista tympanica extends only very slightly into tympanic cavity	crista tympanica projects into cavity; moderately long tubular meatus

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8. ventral edge of ectotympanic finished, faceted	extent of ectctympanic not determinable
12. bulla not completely ossified	bulla fully ossified and complete
13. entotympanic thick, sandwich construction with cancellous interior	entotympanic not demonstrated; bulla wall thin, unilaminar, solid bone
16. hypotympanic sinus never invades mastoid	hollow in mastoid enlarges hypotympanic sinus
17. no cristae on internal surface of entotympanic	several variable crista on internal wall of bulla
18. auditory region deeply recessed	shallow auditory region
22. petrobasilar foramen: bony partition separating exit of inferior petrosal sinus	exit of inferior petrosal sinus internally confluent with posterior lacerate f.
24. postglenoid for. present	postglenoid for. absent

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28. anteromedial buttress on basisphenoid; no anteromedial process from bulla	typical anteromedial process present; no buttress on basisphenoid
29. vertical flanges on basioccipital medial to bulla	no vertical flanges; basioccipital overlies bulla
30. little ossification of tentorium ventrally	broad ossification of tentorium next to petrosal
31. dorsal basioccipital flange roofing petrobasilar canal	open inferior petrosal sulcus on dorsal surface of basioccipital
32. mastoid foramen present	mastoid foramen absent
33. postparietal for. present	postparietal for. absent

Similarities between Barbourofelinae and other nimravids

Barbourofelis does share the following features with the other nimravids examined. Again, the homologies and polarities will be discussed in the next section.

2. crista tympanica is oriented in a vertical or nearly vertical plane, about 30 to 45 degrees from sagittal plane

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3. external auditory meatus is wider than tympanic notch and therefore is partially blocked anteriorly by postglenoid process

7. processus tubarius present on anterior crus of ectotympanic

11. no septum bullae is present

15. posterior carotid foramen through wall of bulla is laterally placed

21. some sort of channel for the anastomosis of the ascending pharyngeal artery with the distal portion of the internal carotid artery is present at the anteromedial corner of the bulla

23. posterior lacerate foramen positioned somewhat laterally (although not as much so as in other nimravids)

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DISCUSSION

Introduction and Apologia

I have found problems at several levels of the analysis in both my own work and with the published literature. The basicranial region is topographically complex, the nomenclature inconsistent, and details of the soft structures or ontogeny for many extant forms unknown. These factors contribute to the problems at the different levels.

First, at the level of "morphology" (data level I in my scheme in Figure 15), there are unfortunately instances of faulty observation or reporting of structures or both. Perhaps inexpert or incomplete preparation created an inaccurate appearance, or perhaps writing the actual report from notes some time after study of the specimen resulted in the discrepancies, but for whatever reasons, instances can be found (although rare, fortunately) of published descriptions that just do not appear to me to accurately describe some feature of a specific specimen.

More commonly, apparent inaccuracies contain a larger element of interpretation. As an example, several authors have argued (e.g. Scott, 1889; Hough, 1953: 106) that a septum bullae is present in some specimens of Dinictis. Examination of the specimens, and often of earlier sections of the published reports themselves, reveal that

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what the authors perhaps saw was the short partition in the anteromedial corner of the bulla. This was interpreted (producing information itself generally considered factual--Level I in Figure 15) as being merely the visible part of a complete septum across the bulla (often incomplete preparation permitted this), which was in turn homologized (producing a hypothesis at Level II) with the septum bullae described by Wincza (1896) in Felis catus. Subsequent authors, gleaning character distributions from the literature as we all must, reported simply that a septum bullae was present in Dinictis, or more often, "in nimravids". At this point, nimravids now apparently share a character considered significant in the definition of the Aeluroidea (e.g. Flower, 1869; Pocock, 1916b; Hunt, 1974, to illustrate the persistence of this judgment)--a character that no one has actually seen. Thus when the initial observation is repeated, and the material carefully prepared, one finds that the initial observation (hypothesis at Level I) was apparently partly right and now partly refuted, and everything following is now considered entirely wrong: there is indeed a flange of bone projecting into the tympanic cavity of Dinictis, but it is a low, partial septum with a finished edge, not even as extensive as the canid septum, and clearly not bilaminar, being entotympanic only.

So part of the problem is the difference between what

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is seen (the anterior projection of bone) and what this is interpreted to be (part of a complete septum). Although it would be easy to preach carefulness and objectivity, as proponents of "the scientific method" are perhaps prone to do, I think it is more important to realize that one always interprets what one sees, and some problems will inevitably result. Perhaps the best antidote is active collaboration among anatomists in the interpretation and description of material (on the assumption that mass hallucinations are rarer events than are individual cases of wishful thinking).

The second part of the problem lies in the act of homologizing the structure--i.e., identifying a structure (step 1 in Figure 15, producing hypotheses at data level II). In this example, I have tested the identification of this structure as a "septum bullae" in the foregoing descriptions by further consideration of its topological relationships and its detailed structure. On the basis of those results, I consider the identification of the structure as a septum bullae refuted for the time being--i.e., I am holding preferentially a competing hypothesis.

The final problem illustrated by this example is that of the breadth of sampling underlying generalizations about conditions within a higher taxon. Here, a septum observed in some Dinictis had been generalized by some

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authors to be true of the entire family Nimravidae. Although generalization is necessary, I have tried to balance it with statements of the relative breadth of the sample underlying each generalization.

I hasten to acknowledge that I have all the above problems with my own analyses as well as with those of some other anatomists. Sometimes people make incorrect identifications because they do not know the structure of such a complex region as thoroughly as they might; it is a rare paleontologist of whom this is not true occasionally. Also, however, the incomplete nature of fossil material, and even of some recent forms for which soft anatomy is poorly known, requires one to constantly evaluate and perhaps revise the identification of features--the hypotheses of homology. Conclusions, reported here or anywhere else, can not be final or certain.

With these caveats or disclaimers behind me, I will now summarize the character analysis of each feature that I was able to recognize and characterize (i.e. formulate hypotheses at level I for a diversity of taxa). Under Step 1 (see Table 4), the structural relationships I thought most significant in making my identifications will be reviewed for each feature about which any reasonable question has been or could be raised, to my knowledge. Step 2 of the analysis--determining the generality of distribution of each character and the nesting of

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characters (including what is meant by the "polarity of a character")--uses information from several sources: the distribution of each feature among other Carnivora, the ontogenetic history of each feature, and the structural and compositional relationships among features.

In order to restrict the scope of this study to a manageable size, I relied on the literature for much of the information about character distributions. Rather than generate yet another narrative summary of the basicranial surveys that have been done in the past, I have instead distilled the portions from the most comprehensive of those surveys that are most comparative--i.e., those which present comparable descriptions of the same structures on a diversity of taxa (Table 6). This is, of course, the sort of information needed for constructing phylogenetic hypotheses on a reasonably objective basis. One conclusion that can be drawn from the results is that the conditions for relatively few characters are well documented across the entire range of diversity within the order. Much work remains to be done. The table emphasizes the extant forms in most cases; the assignment to family of many fossil forms is disputed because of the larger number of more generally shared, primitive characters in many fossil taxa, and fewer synapomorphies with the extant representatives. As a result, the distribution of

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character states would be much harder to summarize for groups that included all referred fossils.

Study of this tabulation reveals two, complementary problems for my analysis. First, some informative features studied intensively over a reasonable diversity of carnivorans are not ascertainable in fossil material. For example, I have concluded that most hypotheses about circulatory patterns in extinct animals are very high order hypotheses, and therefore both based on relatively tenuous evidence and relatively difficult to test. The second problem is that several of the features identified in my detailed analysis of these few taxa are not mentioned in the literature on other carnivoran taxa. I have therefore examined some additional specimens, but must emphasize that this was necessarily limited. In these comparisons, I concentrate on taxa that are more likely to represent out-groups: miacids, viverravids, and creodonts. And I have relied heavily on the very useful analysis and summary by MacPhee (1981) for primates and eutherian insectivores, in which an analysis of the primitive condition of many features in eutherians was presented. (I will therefore not reiterate a discussion of the basic eutherian morphotype and polarities for eutherians here.)

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Tympanic Floor: Ectotympanic

1. All living therians have an ectotympanic, which always arises intramembranously (Van der Klaauw, 1931: 6; MacPhee, 1981: 19). I know of no evidence that has cast doubt on the homology of this element within therians, much less within carnivorans. The ectotympanic is usually readily identified by the presence of a meatus, crista tympanica, and the constant relationship with adjacent cranial elements--the anterior crus inserts on the squamosal and the posterior crus on the anteromedial corner of the mastoid process. I have, however, to my surprise, found one case of disagreement with the identification of an ectotympanic as being that element: Van der Klaauw (1931: 316-318) argued that the element previously identified as an (ecto)tympanic ring in a particular skull of Nimravus was perhaps the remnant of a septum instead, perhaps even of a septum bullae. From his description, I conclude that incomplete preservation or the presence of obscuring matrix or both resulted in an inaccurate assessment of critica features; in the more completely preserved and prepared specimens, one can see that a complete crista tympanica does indeed occur on the inner face, that the anterior crus is elongate and dorsally returns to the correct point of insertion just medial to the postglenoid foramen, and that there is a suture separating the posterior crus from the caudal

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process of the petrosal, for example. An erroneous level I hypothesis resulted from not recognizing these features.

The primitive form of the ectotympanic is quite uncertain: MacPhee (1981: 252) tentatively proposed that some expansion is probably primitive, especially the ventrolateral rim, and that no expansion or great expansion would then both be derived. Van der Klaauw (1931: 10-11) reviewed various authors' statements about whether ringlike or broadened ectctympanics are primitive for Carnivora and Creodonta, demonstrating that there has been a fair amount of confusion or ambiguity about what is meant by "ringlike". Both very expanded (both medially and laterally) and only moderately expanded ectotympanics are found among carnivorans; arguing from the relatively little expansion of the ectotympanic scattered throughout marsupials and eutherian insectivores, limited expansion be primitive for Carnivora.

The nature and direction of that expansion, however, can also show variation. The moderately expanded condition that has just been argued to be primitive is one of medial expansion, producing (if an entotympanic is absent) a shieldlike demi-bulla. The platelike appearance of the nimravid ectotympanic seems to me to correspond best to Van der Klaauw's "ventral expansion", (which elsewhere occurs sporadically in xenarthrans); yet even this potential similarity is not clear, however, because

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in Van der Klaauw's own analysis of a Nimravus basicranium (discussed above), he found the shape and position of the ectotympanic so odd that he decided it was really the remnant of a septum in the bulla. Yet what he described sounds like every ectotympanic I have seen in Dinictis, Nimravus, or Hoplophoneus. Given its limited distribution outside the Carnivora, and restriction within the order to nimravids, this platelike condition of the ectotympanic would appear to be derived for nimravids.

Comparison with miacids (s.l.) and creodonts offers no help in this feature. No miacid has been found with the ectotympanic preserved. Few creodonts have ectotympanics preserved (the one I am studying does not) and the literature is very contradictory about their condition. Ontogeny does not seem to offer an answer either: MacPhee (1981: 252) argued fairly convincingly against the hypothesis that the very simple ringlike condition seen in tupaiids and lemurs is the primitive adult condition for therians.

I can see no structural restrictions on this feature. That it is not an automatic correlate of the lack of an ossified entotympanic is of course demonstrated by forms such as Nandinia, Dasypus, or the megachiropterans Pteropus, Acerodon, and Boneia (Novacek, 1977), in which the ectotympanic is more shieldlike. Barbourofelis might share this condition if the ectotympanic were only the

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lateral-most, vertical portion of the bulla; this cannot be determined until the limits of the ectotympanic are determined. And of course, even if the bulla in Barbourofelis were found to be entirely ectotympanic, this could be an even more derived condition developed from that seen in the other nimravids. The condition of the bulla in Eusmilus and Sansanosmilus will be very relevant to these questions; additional study is needed, particularly of these latter taxa.

2. A nearly horizontal inclination of the tympanic membrane, as judged from the inclination of the tympanic ring, is widely considered primitive (e.g., Van der Klaauw, 1931: 16, and references cited therein), on the basis of both its wide distribution and its initial position during ontogeny. At first I thought MacPhee (1981: 246) held the opposite opinion, because he listed the primitive state as "highly inclined," which I contrasted with Van der Klaauw's (1931: 16) "nearly horizontal tympanic ring...this small inclination." However, I find that whereas Van der Klaauw was speaking of inclination from the horizontal, MacPhee was evidently referring to inclination from the vertical: "the angle between the horizontal and the plane of the ectotympanic...is at first quite small and the ectotympanic is highly inclined" (MacPhee, 1981: 23). I conclude that the term "inclined" must be well qualified

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and is probably best avoided at this point.

Although I did observe that the plane of the annulus in nimravids is quite vertical, I have not seen any specimen matching Van der Klaauw's (1931: 316) observation in his specimen of Nimravus that the annulus was actually tilted the other way, from dorsomedial to ventrolateral. He indicated that he saw that condition in no other mammal. (He did not object to the ectotympanic's angle from the sagittal plane in the Nimravus he was studying; this matches my observations that the oblique angle is very standard within Carnivora and elsewhere.)

Van der Klaauw (1931: 16-18) documented some variation in the degree to which the ectotympanic is vertical in different mammalian orders, but in general concluded that it is exceptional in adults for the tympanic ring to be horizontal. Within the Carnivora, those with inflated bullae generally have rings oriented between 45 degrees and nearly vertical, whereas those with flat, relatively uninflated bullae, such as lutrines or melines, have a crista tympanica that forms much less than a 45 degree angle with the horizontal. Reference to miacids or creodonts is again of no help. The distribution of the feature in ontogeny is, like the shape of the fetal ectotympanic, very consistent and supports the hypothesis of a horizontal orientation being primitive for Mammalia but gives no further clue about the polarity

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within the order Carnivora. In a sense, the horizontal orientation is very directly a function of the bulla shape in those carnivorans with a flattened bulla, and perhaps it is the latter feature that should be analyzed. In any case, the only evidence I can find for the polarity of this feature is that the vertical orientation is an extreme condition and therefore probably derived--not a very strong argument. Because of this uncertainty as well as a lack of definition of states of this feature for other Carnivora, I consider this character uninformative at present.

3. When Van der Klaauw (1931: 317) observed that the horizontal diameter of the external auditory meatus in his specimen of Nimravus was so much larger than the tympanic notch was wide, he used that as an additional objection to the identification of that bone as the ectotympanic, and asserted that "If it really is an annulus tympanicus which is out of place, its shape must have changed..." From my observations, I have concluded that the ectotympanic was probably undistorted and in proper position in his specimen: every nimravid specimen I examined in which the ectotympanic is not actually broken or absent exhibited this condition. In every case, the very long horizontal anterior crus lay appressed to the squamosal along an area the anterior end of which is very far anteromedial to the typical insertion for the crus (as Van der Klaauw

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observed), but of which the posterior end is in the proper position. I have concluded from this feature's constancy and the lack of contradiction when the full ring is considered that this represents the condition of the ectotympanic in life in these animals.

I have not seen this condition in any non-nimravid mammal (nor apparently had Van der Klaauw), nor can I find any other reference in the literature to it in either nimravids or other mammals (although Hough, 1953, did note that the nimravid meatus faces into the base of the postglenoid process, a relationship that results from the shape, size, and orientation of the tympanic ring in this case). I conclude therefore that this is a specialized condition for nimravids including Barbourofelis.

4. A projection of the tympanic crista and sulcus well inside the bulla was mentioned by Van der Klaauw (1931: 202) for some carnivorans, rodents, and ungulates. There appears, from his comments, to be much variation in the structural details of what this projection actually is and its relationships with adjacent bulla topology. My survey of the other Carnivora was too limited to demonstrate whether or not distinctly different states of this feature could be recognized. In non-nimravid carnivorans, extension of the crista tympanica is often much greater ventrally than dorsally, further complicating definition of states. Frequently, the apparent expansion

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seems to be a function of some combination of the angle at which the tympanic ring is inclined from the vertical, and the degree and manner of expansion laterally to produce an external auditory meatal tube, as well as the projection of the crista itself. Therefore the main problem with this feature at present is the lack of definition of character states.

As with previous ectotympanic features, miacids and creodonts supply no information about other states or polarity. Ontogeny indicates that any extension develops secondarily. Given the distribution in general within the Mammalia, the simplest hypothesis appears to be that the nimravid condition (except Barbourofelis) is primitive for the Carnivora (and therefore will not supply direct evidence of relationship), but I do not know the variation well enough within the order to argue for any special resemblance between the particular derived condition in Barbourofelis and any other carnivoran taxon, or among other carnivoran taxa such that the Nimravidae are excluded from particular groups.

5. A closed or nearly closed tympanic ring, in which the two crura meet or nearly meet above the external auditory meatus, is difficult to demonstrate if there has been extensive co-ossification with the squamosal, as is the case, for example, in Barbourofelis. In the other nimravids, the sutures outlining the crura are still

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visible, and one can determine that they come within a few millimeters of meeting dorsally, because of the horizontal elongation of the anterior crus.

The closed or nearly closed condition, according to Van der Klaauw (1931: 14-16), occurs in Chiroptera, xenarthrans, many rodents, Viverra, Canis, Putorius, Mustela and perhaps Phoca among the Carnivora, and Tarsius, and many ungulates (in which the tube is often greatly elongated). Several points are not clear from a list like this: whether there really are two distinct states--half a tube as in Ursus and a closed tube or nearly so as in Canis--or, since it is not clear what taxa were examined and which lacked the closed tube, whether intermediate states occur (as would seem likely), and if so, how much variation there is within a species or genus. However, the the few specimens I examined (Table 3), there did indeed seem to be two states, separable on whether the anterior crus was bent and had a horizontal segment (resulting in a closed or nearly closed ring) or whether it was simply posterodorsally directed (U-shaped ectotympanic). And the distributions of these states were apparently largely consistent within families--apparent, that is, to the extent that fusion of ectotympanic with squamosal did not obscure the condition.

The ursids and procyonids quite clearly had troughs of ectotympanic roofed by squamosal (as did Amphicyon).

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Mustelids all had a completely closed tube; although co-ossification was frequently extensive, there was always a line of pores and ridges that appeared to delineate the edge of the ectotympanic. Canis latrans clearly had a completely closed tube (as did the canids Segal, 1943, examined), whereas Hesperocyon had an open, U-shaped tympanic ring (which, together with the open 'ring' in several other Oligocene carnivorans, suggested to Clark and Guensbery, 1972, that closure occurred independently in several families and was not a reliable phylogenetic indicator). The Viverridae consistently had an open, U-shaped ectotympanic, whereas Herpestidae had a closed or nearly closed ring like the Hyaenidae.

The only family in which variation in this feature was seen (among extant forms) was the Felidae. The crura of the ectotympanic fused at a very early age to the squamosal in felids; this combined with the formation of a sharp ridge on the squamosal creates a strong impression of a closed ring in Felis catus, which is disproven when the skulls of kittens are examined. In the latter, the ridge of squamosal is evident at a very early stage. However, in other specimens (Panthera tigris AMNH CA 1798, for example), the outline of the crura were still evident; in this case the crura met at the posterior edge of the dorsal rim, closing the tympanic ring.

As with other features of the ectotympanic, the

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degree of closure of the tympanic ring is not known for miacids or viverravids, and was not reported by Van der Klaauw (1931: 145) for any of the taxa we now recognize as creodonts. Although the lipotyphlans and primates generally have incomplete U-shaped ectotympanics, a complete bony tube is widespread among the Mammalia, especially among the ungulates, so the distribution as a whole does not argue strongly for either polarity. Ontogeny suggests that an open, U shape is most generally distributed. This is the polarity I have tentatively accepted for the character for the present, but I think that the condition in creodonts, miacids, and other possible out-groups to the Carnivora will also be important to consider when complete ectotympanics are found.

6. As with the previous character, the degree of expansion of the posterior crus is determinable only when co-ossification is not so extensive as to obscure the limits of the element. Thus, I could determine this feature--lack of expansion--with fair certainty for all nimravids examined except Barbourofelis, as long as the region was very free of matrix. This actually was a serious limitation in this region because of the difficulty of cleaning the complex, crevassed area.

Based on both the condition early in ontogeny, and the distribution of horseshoe-shaped ectotympanics in

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mammals, the unexpanded posterior crus is probably primitive. The distribution of this character is clearly closely related to the distribution of the previous one, and to the amount and pattern of medial or ventral expansion of the ectotympanic, but also to the relationship between the ectotympanic and the processus hyoideus. Co-ossification obscured this feature in the majority of Recent specimens I examined, and I was therefore unable to establish character states and distributions within the Carnivora.

7. The only mention of the processus tubarius on the ectotympanic that I have found is Van der Klaauw's (1931: 132) brief discussion. (Gray's Anatomy, 1980, identified a processus tubarius on the ventral surface of the medial pterygoid plate, describing it as an angular process that supports the pharyngeal end of the auditory tube. This is clearly not the homologue of the process labelled by Van der Klaauw as the processus tubarius. Since the term does not seem in widespread use in the literature on the anatomy and paleontology of carnivorans, perhaps an alternative term should be adopted.) I have identified the medially-directed process from the anterior crus of the ectotympanic in nimravids as a processus tubarius because it is an ectotympanic process, and is in the correct general position to correspond to Van der Klaauw's process (see Figure 43). It differs in orientation and

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details of position from the processus tubarius in the feloids: in the latter, the process is hooklike, so that the end points up the canalis musculotubarius (except in Hyaenidae, in which the process is a mere nubbin). In one of the dissected domestic cat ear regions, the tendon of a muscle, presumably the tensor veli palatini, was still attached and headed up the canal. The hook is not appressed to the roofing elements, but projects out clearly ventrally to them, often beneath the fossa muscularis major or even its anteromedial edge.

Because of a lack of suitable dissected specimens (and a more difficult ear morphology to open), I am less certain of this feature for the caniforms. I have not yet found a processus tubarius in any mustelid and have not been able to determine presence or absence for ursids. In Nasua and Canis, I think I can see a medial process from the ectotympanic, in this case lying appressed to the roof between the epitympanic recess and the fossa muscularis major. In Miller et al. (1964), I find no mention of such a process. On page 156 of that reference, the tensor veli palatini muscle is described as originating on the styliform process of the bulla. However, on p. 855, the tendon of the muscle is illustrated in the canalis musculotubarius, extending back beside the fossa muscularis major; on page 253, the muscle is said to arise "in the groove of the petrous temporal bone ventrolateral

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to the tensor tympani muscle." The process from the ectotympanic lies ventrolateral to the fossa for the tensor tympani muscle.

My present hypothesis is that these are all processi tubarii, and that the nimravid condition is specifically like the condition found in at least some canids and procyonids, on the basis of its orientation and relationships to the features in the tympanic roof.

A similar hook (like the condition in Felis) was mentioned for Cervidae and Tapirus by Van der Klaauw; the condition in cetaceans is less clear. I hypothesize that the presence of the process is derived for the order Carnivora, but recognize that its distribution, especially within the caniforms, needs to be more carefully and completely mapped.

8. To describe the ventral edge of the ectotympanic as finished and faceted is to make a judgment about the regularity of the shape of the edge. Several of the nimravid specimens I examined had bilaterally symmetrical ectotympanics, with either a beveled edge, rugose as if for the attachment of a thick cartilage, or an edge with a shallow sulcus in the middle of the flattened, widened part. None of these sulci were ever as deep in the ventral and anterior portions as the deeply grooved edge of the ectotympanic in Nandinia, so there is not a complete parallel there. Since all eutherians have a

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fibrous membrane flooring their auditory region (MacPhee, 1981), I presume that at least such a membrane attached to this surface. The full arguments about a cartilage versus membrane floor will be discussed later in the consideration of the entotympanic.

In conclusion, it is uncertain whether this flattened edge is the same character state as the edge of the ectotympanic in Nandinia, but I think it unlikely. I have not seen a Daphoenus ear region with the edge of the demi-bulla intact; however, judging solely from the shape and orientation of the ectotympanic in daphoenids, it appears to be much more like that of Nandinia than like that of the nimravids.

This feature is obviously closely linked with the incomplete ossification of the bulla (and is here conservatively considered part of that character in the phylogenetic analysis), and can therefore be considered to have the same polarity: the condition in nimravids is hypothesized to be derived (see the argument in the entotympanic discussion). The lack of specific similarity in the angle and structure of the edge neither precludes the nimravid condition from homology with that of Nandinia and daphoenids, nor does it provide specific evidence for such a homology.

9. The presence of an ossified tube (pars ossea tubae of Van der Klaauw, 1931: 136) or trough (roofed by

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sphenoid) for the canalis musculotubarius is widespread within the Carnivora, and only questionably scattered throughout other orders. In a number of cases, Van der Klaauw described a tube formed partly by the styliform process, which does not seem to me the same condition as a fully ossified, completely walled tube or trough. The latter condition was described for carnivorans, for Elephas, and questionably for a few ungulates.

Again, the definition of "the same" character state is not well resolved in my estimation. Almost all of the Carnivora have fully ossified and expanded (although not necessarily ventrally inflated) bullae, which as they expand anteriorly will come to underlie the canalis musculotubarius. Complete ossification of a bulla requires that the auditory tube, m. tensor veli palatini, and associated structures pass through some sort of aperture at the anterior margin of that bulla. It is interesting to me that, although the rostral entotympanic cartilage is closely associated with the cartilage of the auditory tube during development, it appears to be usually, if not always, the ectotympanic that in Carnivora forms the bony trough or tube for the canalis musculotubarius. So, although formation of a tube might be a mechanical outcome of how carnivorans formed an ossified bulla, that the tube is ectotympanic is slightly surprising and argues that the osseous tube is a character

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distinct from the ossification of the bulla itself.

Another consideration relevant to the distinctness of the character is the condition of this tube in taxa retaining cartilaginous entotympanics, especially since that is hypothesized to be the condition of the ventral part of the entotympanics in the nimravids. In Nandinia, there is no formation of an osseous tube, nor does there appear to have been one in Daphoenus, judging from the one cast that is available to me. The condition in nimravids is both different and variable: in Dinictis and Hoplophoneus, there is usually a bony extension (usually emarginate ventrally) and a partial trough, walled posteromedially also by the curled end of the entotympanic. (However, in at least one specimen of Dinictis, USNM 15889, the ectotympanics look complete but are shieldlike with no anteromedial osseous tube or even extension. very much like the condition in Nandinia.) In Nimravus, complete, ossified, ectotympanic troughs extend far anteromedially.

Perhaps the presence of some ossification of an entotympanic wall is an developmental inducer that triggers the ossification of the tube in carnivorans; faceting on the basisphenoid indicates that the entotympanic extended all the way anteriorly in nimravids, even in those specimens in which preservation has not been complete. However, Nandinia has an ossified rostral

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entotympanic so the form of the ossification must be significant as well.

A possible hypothesis is that it is specifically an ossified caudal entotympanic forming a wall medially that triggers development of an osseous tube. This is suggested by my observation that in modern carnivoran bullae the caudal entotympanic forms the anteroventral cup of the bulla, and hence the medial wall of the pars ossea tubae, and that the rostral entotympanic is rather restricted to the medial side of the bulla, and usually dorsally placed. In one, fully adult specimen of Viverra, (AMNH CA 91) a distinct rostral entotympanic is visible dorsally and clearly not involved in the anterior wall of the bulla proper. The topology of this region is very similar among a great diversity of carnivorans, and if the extensive co-ossification between ecto- and entotympanics in most carnivorans is considered (as well as the complete ventral ossification in most carnivorans, of course), it will be realized that the shape and relationships of the entotympanic and ectotympanic in the anterior portion specifically of the nimravid ear is not particularly unusual. It is the lack of co-ossification among elements and incomplete ossification of the entotympanics ventrally that are unusual.

The preceeding arguments and observations are also additional, although very indirect, evidence that the

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cartilaginous entotympanic condition in nimravids is independent from that in Nandinia and daphoenids, since the details of the anatomy are different and some aspects of the nimravids (the ossified tube) are more like the states seen in other Carnivora. Furthermore, to reiterate one point, if my suggestion of induction is correct, it would require that the entotympanic ossified in nimravids be specifically a caudal entotympanic.

Among Carnivora, according to Van der Klaauw (1931), mustelids, ursids, and procyonids have tubes completely surrounded by ectotympanic, whereas the troughs in canids, viverrids (including herpestids?), hyaenids, and felids are all roofed by alisphenoid, as is the canal in nimravids. Based on merely transformationist arguments (see methods section), if the presence of a tube is derived for Carnivora (as appears to be the case on the basis of distribution), then the more complete tube would be most derived, excluding nimravids from membership within the Arctoidea (but not as a sister group to that group, of course).

10. Van der Klaauw (1931: 133-136) documented a wide occurrence of a styliform process, pointing out that it may be formed from ectotympanic, entotympanic, or petrosal bones. In my investigation, I have found its presence and degree of development variable within taxa, and its identification by other workers unreliable (e.g., I

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believe the anteromedial prccess of the bulla has been consistently misidentified as a styliform process, especially in Felis--see Glossary). Therefore, I conclude that the definition of the states of this feature is nowhere near complete, and from the sorts of variation seen, it might not be particularly informative were the effort made. I see no way of judging polarity when the states are not adequately defined, since some sort of process is widespread but apparent absence is not obviously primitive in this case.

11. Presence or absence of a septum bullae in nimravids has been a subject of disagreement for the last century. The belief has apparently been strong that a septum bullae should be present, because the nimravids were considered to be obviously cats. Although he had been unable to find a septum in his earlier studies (1880a), Cope (1882) later implied by his key that the Nimravidae had a septum bullae (even while indicating the belief prevalent at that time that Hyaenidae did not). Scott (1889) thought that a complete septum was present. Van der Klaauw (1931: 317) misidentified an ectotympanic in Nimravus as a septum, perhaps a septum bullae. Hough (1953) presented the opposite situation from that of Cope: she identified a low broken ridge in a specimen of Dinictis cyclops as being the remnant of a septum bullae (p. 106), but concludes seven pages later that the bullae

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of Oligocene felids were "simple and without a septum" (p. 103). Brunet (1967: 9) described a septum in Dinictis as being in an identical position to that of Canis. (He called the septum in the latter a "septum bullae" as well, even though recognizing it is unilaminar, so evidently he did not mean by the term the very specific structure intended by Winge (1896), Van der Klaauw (1931), and Hunt (1974a), for example.) Clark and Guensburg (1972) reported the anterior part of a septum bullae (their term) in both Hoplophoneus and Dinictis, and argue that "Since the septum bullae lies at the juncture of the entotympanic with the tympanic proper, these specimens prove that both elements were developed and ossified in the Oligocene felids."

As described above, I can find no evidence in nimravids, either direct or indirect, of a complete septum, much less a true septum bullae. The ectotympanic exhibits a finished edge ventrally, and was therefore not curved over to form a dorsally directed partition. The recurved anterior entotympanic is merely forming the anterior wall of the tympanic cavity, separating it from the canalis musculotubarius, much as one sees in a completely co-ossified form in many arctoids. This anterior wall of entotympanic also displays in a few specimens a smooth, unbroken edge indicating that the portion of entotympanic preserved is complete, so it was

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not nearly as extensive, nor in the same position, as even the septum in Canis latrans, for example. I have examined most of the specimens reported on by Hough (1953) and Clark and Guensburg (1972) and see only this anterior edge of entotympanic if anything. Therefore I conclude that there was no septum at all in the nimravid bulla, and certainly not a septum bullae proper.

Hough (1953: 106) also cited some indirect evidence in Dinictis arguing for the presence of a septum across the bulla. However, in contrast to Hough's observations, I can find no grooving or flattening on the promontorium in any nimravid that would clearly indicate a complete septum. This, however, is not decisive, because neither felids nor viverrids invariably have traces on their promontoria indicating the septum that is present in those taxa. The septum bullae, when present, represents upturned edges of both ecto- and entotympanic, and thus is continuous ventrally with the bulla itself (see Figure 47), but dorsally does not typically contact the promontorium in felids, and not always in viverrids. Instead, at least in felids, a passage remains, which may vary from a low aperture to a very narrow slit, between the curled edge of the septum and an indistinct facet on the ventral-most surface of the promontorium; across this slit may run connective tissue or fascia of some sort. (Some fibers, for example, are still visible in the left

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ear of the Felis catus, the other side of which was illustrated in Figure 43, AMNH AINS-589.) Based, therefore, on the conditions seen in modern aeluroids, the absence of a facet on the ventral surface is uninformative about the presence or absence of a septum.

Hunt (1974a) established the nature and distribution of the major types of septa within the Carnivora. That of the Feloidea, except for Hyaenidae, is this bilaminar septum bullae, produced by the upturned margins from the ventral edges of the ecto- and caudal entotympanic (A in Figure 48). That of the Hyaenidae was considered by Hunt (1974a) to be probably unilaminar and ectotympanic (B in Figure 48), but this has not been well demonstrated yet. Finally, the partial septum in Canidae is entotympanic, but is from the dorsal (and anterior) edge of the caudal entotympanic, according to Hunt (1974a: 38), rather than from the ventral edge as was the caudal entotympanic contribution to the septum bullae. Here is a good example of strong evidence at the level of character analysis that two features that might be considered the same--the caudal entotympanic septum in canids and the caudal entotympanic contribution to the septum bullae in most feloids--are actually different states, since they are fundamentally different in their origins if Hunt's analysis is correct.

This character, then, shows several definable states for which we can now consider construction of a character

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state tree. The septum bullae has not been found outside the Carnivora, and is therefore considered here a derived feature within the order. A variety of cristae and partial septa, usually quite variable, occur in the entotympanic portion of some arctoid Carnivora, and in the bulla of a variety of other eutherians; it is therefore not clear from distributional information whether the mere presense of such cristae is primitive or derived. I suspect there are several character states still to be distinguished. In contrast to these variable septa, the structure of the partial septum in the Canidae is remarkably consistent, and the method of development is not yet documented elsewhere to my knowledge. I therefore conclude that it too is a derived feature (and derived independently of the entotympanic contribution to the septum bullae, as discussed in the previous paragraph). This conclusion is in contrast to Scott's (1889: 234) description of the "primitive carnivorous skull" in which a septum like that of Canis or even one more complete was present. This is a conclusion predicated, of course, on a failure to distinguish among the different kinds of septa present in the carnivorous bulla.

The question now remains of the relationship of the hyaenid septum to the other carnivoran septa. It is important to emphasize that the basic character state has not been well demonstrated: Hunt (1974a: 42 and 43)

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expressed considerable uncertainty about the composition of the hyaenid bulla. There appear to me to be three possiblities for the relaticnship of the hyaenid condition to the others if it is taken to be a unilaminar, ectotympanic septum: such a septum could be an independent derivation (A in Figure 49), it could be a modification of the septum bullae by loss of the entotympanic contribution tc the septum (B in Figure 49), or it cculd be a more general feature which includes the septum bullae as a particular modification via the addition of the entotympanic layer to the septum (C in Figure 49).

At this point, the best choice among these three is not obvious. Trees B or C are perhaps preferable to A because we have no evidence suggesting that the ectotympanic hyaenid septum is in any way different from the ectotympanic portion of the septum bullae. Comparison of the diagram of the developing hyaenid bulla (B in Figure 48) with the bulla of a felid, herpestid, or viverrid (A in Figure 48) suggests that differences in position and relationship with adjacent elements are due to different relative amounts of inflation of the ecto- and entotympanic portions. Pocock (1916b) pointed out the consistency in several very significant relationships: the hyaenid septum extends from the medial pcrtion cf the mastoid, just as does the septum bullae, and the "dorsal

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edge" of the septum, that nearest the petrosal, leaves a gap near the aperture of the cochlear fossula. Therefore, until we have some evidence to the contrary, it seems simplest to consider the ectotympanic septa in hyaenids the homologue of the ectotympanic portion of the septum bullae.

This conclusion requires, however, that the septum bullae be actually a compound feature, in the sense that its derivation from a state of no septum is a two step change if we are counting events on an evolutionary tree, and thus tree C is the shortest of the three and the most parsimonious hypothesis from character analysis. I would argue, however, that not only do we need to establish the character state in hyaenids more clearly before putting much weight on these conclusions, but details of the development of the septum bullae itself could provide some useful evidence about the true complexity of the feature. (For example, does the ectotympanic in the young of an animal typically possessing a septum bullae still independently form a septum if the entotympanic is removed or is an interaction between the two elements required?)

The implications of this character are important: the septum bullae is a very consistent character uniting three of the four families in the Feloidea, and a complete septum of at least ectotympanic characterizes the Feloidea as a whole. This septum is a very consistent feature,

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either reduced or absent in only one species (Nandinia), and clearly absent in all Nimravidae, thus excluding the Nimravidae from close phylogenetic relationships with any group within the Feloidea.

12. Hough (1952: 97) argued forcefully that the broken fragments of bulla and the impressions on the bones adjacent to the nimravid ear were evidence that the nimravid auditory bulla was originally "complete, fully ossified and similar in shape and size to that of the Canidae". She reasoned that the single-chambered canid-like bulla was fragile and easily broken, and therefore rarely if ever preserved intact. Earlier authors had apparently simply assumed an ossified bulla was present (e.g. Adams, 1896: 421: "the bullae are seldom preserved"), while subsequent authors usually followed arguments similar to Hough's (e.g. Brunet, 1967: 9; Hunt, 1974b: 1039).

One exception to this almost universal opinion was Martin's (1980: 152) observation that in nimravids "the bullae were incomplete with a large entotympanic and a small ectotympanic", and that "the ventral wall of the bulla was cartilaginous". Martin, however, presented no evidence for his divergent opinion, nor for his assertion that cartilage had been present, which of course could not be direct observation.

My observations provide, to my knowledge, the first

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direct evidence supporting Martin's opinion that the bullae were incomplete, but offer only circumstantial (i.e. highly interpreted) evidence about the nature of the tympanic floor--membrane or cartilage. In a well preserved specimen of Dinictis, the smooth, finished, unbroken ventral margins of the bilaterally symmetrical entotympanics demonstrate that the latter are indeed entire ventrally as preserved. This conclusion is corroborated, of course, by the finished ventral margins on several ectotympanics. Indirect evidence precludes the likelihood of a separate ventral bony element joined by cartilage or membrane to those elements preserved: not only do we lack any evidence for such an element, but several specimens prepared for this study have ear ossides or hyoid elements preserved and yet no trace of any bony flooring element. I conclude that the entotympanic in nimravids (excluding Barbourofelis) were ossified as observed, in a broad crescent on the medial, posterior and, to some degree, posterolateral margins of the ear region, and extended only a short distance ventrally beyond the margins of the ear; the tympanic capsule was floored by either fibrous membrane or cartilage.

Of course, only indirect evidence remains to indicate whether membrane or cartilage formed the floor of the tympanic cavity. The flat, medially facing edge on the ectotympanic is several millimeters wide, and in some

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individuals smooth but gently pocked as if a thick cartilage inserted on its face, while in others it has a sulcus through the center of the edge, much like that of Nandinia, although generally shallower and more ventrally directed. The finished ventral edges of the entotympanic in Dinictis are the full thickness of the bone (i.e. they do not taper to a thin edge) and are gently sulcate (see Figure 28). I think that the nature of these margins--both ecto- and entotympanic--indicate cartilage rather than membrane, but the evidence is far from conclusive.

Nandinia is the only living carnivoran known to have typically a partly unossified and therefore partly cartilaginous entotympanic portion of the bulla. Unlike the nimravid entotympanic, the ossifications in this part of Nandinia's bulla are identifiable as a rostral entotympanic--a fully ossified wedge of bone around the internal carotid foramen, dorsal to the anteromedial portion of the bulla--and sometimes irregular patches of bone in the ventral floor of the cartilage that Hunt (1974a) interpreted as multiple ossification centers within the caudal entotympanic. Very different from Nandinia, the ossification of the nimravid entotympanic is much more dorsal, overlapping the promontorium like the dorsal edge of any carnivoran entotympanic, extending around the posterior margin, and neither obviously

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associated with the internal carotid foramen nor appearing to be irregular patches of ossification within a cartilage. Thus there is no particular similarity between the partly cartilaginous bulla of Nandinia and the (putatively) partly cartilaginous bulla of nimravids beyond the mere presence of cartilage.

The number of elements in nimravids is not altogether clear. The main entotympanic described above is seldom complete anteriorly, but in the two Dinictis in which it curls around to cup the anteromedial corner of the bulla, the bone is porous and there is some indication that a second ossification center was present. In Figure 30, the two portions have been indicated. I am reluctant, however, to identify the anterior piece as a rostral entotympanic because it is too far ventral, it is not particularly associated with the internal carotid foramen, and I am not sure whether it is really a distinct element or merely the result of breakage or incomplete preservation. It is not very consistent in shape between the two specimens (AMNH 6937 and F:AM 104823), and is not evident at all in the juvenile Nimravus (F:AM 99259) (but much of the rest of the entotympanic is missing in the latter). In sum, based on present evidence, I am not willing to hypothesize the presence of a rostral entotympanic in nimravids.

The homology of the main part of the ossified

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entotympanic is another major question related to the earlier discussion of the pattern of ossification in Nandinia. Not only does the pattern of ossification and the shape of the resulting entotympanic not resemble either Nandinia or any known ontogenetic stage of carnivorans with fully ossified bullae as adults, but the nature of the bone itself is not known elsewhere among the Carnivora. The nimravid entotympanic exhibits a distinctive sandwich construction, with a very thin layer of bone on either side of a rather thick space sparsely filled with open, cancellous bone (see Figure 28). In short, the only two similarities I can find between the nimravid entotympanic and that of other carnivorans are simply the fact that it is bone, and its relationship dorsally with the promontorium (the entotympanic contributes to the roof of the auditory region in a typical fashion for carnivorans). The first is not a very specific similarity, and the second is also a dissimilarity in the sense that the entire nimravid entotympanic is similar only to a specific portion of the entotympanic of other carnivorans, one that is never found elsewhere independently. Therefore, I conclude that the nimravid "entotympanic" is not the same bony element--is not homologous to--the entotympanic of other carnivorans.

This is all part of a larger question about the homology of entotympanics in eutherians and what structure

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of the bulla is primitive for the entire order Carnivora. The composition of the auditory bulla in eutherians has been much discussed and reviewed in recent years (see Novacek, 1977, and MacPhee, 1981, for summaries and references). Although a couple of his supporting arguments have a dubious logical basis (see Methods, above), Novacek's (1977) main points in his discussion of the origin of the eutherian auditory bulla are still well supported by the remaining arguments, and I therefore agree with his concluding hypothesis--that the primitive eutherian bulla was devoid of ossified entotympanics and had a membranous connection between the ectotympanic ring and the medial wall of the ear region. Beyond this, Novacek (1977), Cartmill and MacPhee (1980) and MacPhee (1979, 1981) all suggested that it is doubtful that all "entotympanics" are homologous across the various orders.

Certainly, however, the composition of the bulla within non-nimravid Carnivora is remarkably consistent, in spite of variations in proportions and structures. Hunt (1974a) was able to demonstrate an entotympanic component in the bullae of every family, both rostral (associated with the internal carotid artery) and one or more caudal entotympanics for most taxa. He hypothesized that a large ectotympanic in an uninflated bulla was primitive for the order. Any inflation he considered derived, some of which occurred in parallel in the different lineages. However,

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if one includes in the analysis the nimravids, miacids, and viverravids, the primitively fully ossified carnivoran bulla of Hunt becomes a synapomorphy uniting the extant families, and clearly not present in the nimravids.

The condition in the miacids and viverravids is less clear: certainly there is not the recessed auditory region seen in nimravids, but that recession, if measured by the relative level of the promontorium and basioccipital, is not found elsewhere in the Carnivora either. What is seen at least to a slight degree, in all extant carnivorans, is the impression on the surrounding bones of the bulla. At least a narrow flat edge is present on the basioccipital and basisphenoid, even if no flange is present, and usually the base of the paroccipital will show a surface of contact. The closest possibility for a facet is visible in Vulpavus (AMNH 11498): at the anteromedial corner of the auditory region, on the ventral surface of the basisphenoid, there is a sharply delimited rugose area, medial to the internal carotid foramen and channel in the sphenoid for the auditory tube. So it is still an open question whether miacids and viverravids had an ossified entotympanic or not. (Certainly there is little if any direct evidence for an ectotympanic in miacids and viverravids, yet it hardly seems reasonable to doubt that at least a tympanic ring was present. Perhaps the entotympanic was as loosely

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attached as the ectotympanic.)

The condition of the bulla in creodonts, as an out-group to the Carnivora, is variable. Various palaeonictids show as little trace of a bulla as do the miacids. Hyaenodon crucians (AMNH 1374) has a very odd, incomplete "entotympanic" and a tympanic wing from the petrosal, quite unlike the condition in the fully ossified bulla of the Carnivora.

In conclusion, I hypothesize here that complete ossification of the auditory bulla via an entotympanic is a synapomorphy uniting most if not all Carnivora exclusive of the Nimravidae (the condition in miacids and viverravids unclear). The peculiar construction of the nimravid entotympanic is treated as another character, derived for the Nimravidae (see below). The number of elements in the bulla of Barbourofelis, or the amounts of their relative contributions to that bulla, is presently unknown. Superficially at least, the bulla resembles the other Carnivora rather than the nimravids in lacking the peculiar construction and in possessing a fully ossified bulla.

It is worth noting as an aside, in the context of the methodology outlined in this report, that the polarity of the condition of Nandinia's bulla relative to that of the other viverrids is subject to wide disagreement. Solounias (1981) cited several references and summarized

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the argument: some consider the cartilaginous condition to be specialized, because some ossification is present, whereas others (including Solounias) consider it primitive "because it resembles an ontogenetically earlier stage and Miacidae" (p. 80). I suggest that we don't know if it resembles the miacid condition or not because so little is known about the latter. But it is quite correct that the resemblance of Nandinia's bulla to ontogenetically earlier stages of other carnivoran bullae does indicate that the condition in Nandinia is more general and therefore primitive. That is the initial step. If, however, other evidence demonstrates that Nandinia is probably closely related to other palm civets and not sister group to all the extant Carnivora, then the ad hoc hypothesis is generated that identifies the specific occurrence of the cartilaginous bulla in Nandinia as neotenous. Our hypotheses of the polarity of the characters in general have not changed--we have not revised lower-order hypotheses to fit higher-order hypotheses--but we have invoked one ad hoc hypothesis in a specific case in response to higher-order parsimony. The distinction is a fundamental one.

13. As described above for Dinictis, Nimravus, and Hoplophoneus, and discussed in the previous character analysis, the entotympanic in these nimravids is of very unusual construction: a thick layer of cancellous bone

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sandwiched between two very thin but very distinct, continuous sheets of bone, so thin as to be sometimes difficult to demonstrate without extremely careful preparation. Whether or not the ossification of the entotympanic is a synapomorphy with other carnivorans, this unique construction can be hypothesized on the basis of its very restricted distribution to be a derived feature (it does not occur to my knowledge in any taxon outside of the Carnivora, nor even elsewhere within the Carnivora). That is, it is autapomorphous for the Nimravidae excluding Barbourofelis. The little available ontogenetic information obtainable from the juvenile Nimravus (F:AM 99259) supports this hypothesis: this ontogenetically earlier stage has a thinner, denser entotympanic, suggesting that the sandwich structure may differentiate secondarily from a less unusual, more homogeneous form of entotympanic. This is an interesting contrast to the nature of the entotympanic in the young of other Carnivora compared with the adult condition there: early in ossification, the bone often has a spongy appearance, described by Hough (1953: 33,36) as cancellous, but with smaller, finer cells than the large, irregular vacuities in the middle layer in the adult nimravid. During ontogeny, the bone becomes denser and thinner.

14. The structure and relationships of the anterior

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edge of the entotympanic have been discussed in the consideration of septa under character 11 above, and indirectly in the analysis of the osseous canalis musculotubarius (character 9). In brief summary, the cupping of the hypotympanic sinus anteriorly by the caudal entotympanic is widespread if not universal among carnivorans with sufficiently ossified entotympanics. The condition in nimravids (again with the exception of Barbourofelis), is not unusual except in the lack of co-ossification between the participating elements. Certainly the anterior margin of the entotympanic in nimravids is not forming a canid septum either. Comparison of Figures 50 (Canis latrans) and 29 (Dinictis cyclops) shows clearly that the canid septum is more extensive, partially walling off an anterior chamber rather than merely the canalis musculotubarius, the dorsal edge being farther medial than ever seen in nimravids.

The lack of co-ossification between ecto- and entotympanics might itself be considered a character. The state is fairly easily defined: the condition in nimravids is immediately recognizable, even in most broken specimens because there are often facets against which the other element abutted. In other carnivorans, the rostral entotympanic is sometimes not co-ossified with the other elements even in the adult, but in all specimens of full adults (in which other sutures such as the

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basisphenoid-basioccipital suture were closed) examined by me, the caudal entotympanic is always fused to the ectotympanic. One may still be able to see a demarcation, but co-ossification has occurred.

The polarity of this feature is more difficult. I know of no other eutherian with a caudal entotympanic abutting the ectotympanic but not ossifying with it, but I do not know the variation in chiropterans, for example, at all well. Again, miacids, viverravids, and creodonts are no direct help; the specimen of Hyaenodon crucians used in this study for comparison has an entotympanic element anteriorly that shows no sign of co-ossification with an ectotympanic, nor does it show any faceting, suggesting to me that it did not even abut an osseous canalis musculotubarius from the ectotympanic, and is therefore a different condition altogether. So the distribution of the feature suggests that the nimravid condition is unique and derived (but this is weak because the distribution throughout eutherians is so uncertain).

In contrast, ontogeny of course proceeds from the non-fused state to the co-ossified state, suggesting that the latter is derived. Finally, there is not immediately apparent any mechanical or structural limitations in nimravids that would create this condition as a side effect.

In conclusion, then, if the lack of ossification

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itself is considered as a character, its distribution within the Carnivora is clear (occurring only in the nimravids, excluding Barbourofelis), but its polarity is not: this feature is either another autapomorphy of the nimravids (which Barbourofelis does not share), or it is a synapomorphy uniting the extant families of Carnivora excluding the Nimravidae.

15. Several specimens of Dinictis and Hoplophoneus had entotympanics that were fairly complete posteriorly and posterolaterally. In these specimens was present a faramen or canal through the lateral part of the posterior wall of the bulla, into the tympanic cavity. (No specimen of Nimravus has yet had preserved an entotympanic complete enough posteriorly to show whether or not such a foramen was present in that genus as well. The single specimen of Eusmilus studied here was lacking the entotympanic entirely.) The presence of this foramen combined with the lack of any identifiable foramen on the medial side of the bulla for a medially placed internal carotid artery presents some extremely interesting implications about the pattern of carotid circulation in nimravids.

Justification for the identification of the petrobasilar foramen as that rather then as a posterior carotid foramen is presented below (character discussion #22). That identification is taken to be correct for the discussion here. Although #22 follows this discussion in

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the text, that is a function of the topological organization of the list of characters; the arguments presented in #22 depend in no way on this character analysis (#15)--i.e. the argument is not circular.

Three possibilities are presented by this laterally placed foramen through the entotympanic: 1) it might have conveyed an internal carotid artery, which would have been laterally positioned and therefore a "promontory branch", 2) the foramen might have transmitted a stapedial artery, and neither a medial nor a lateral (promontory) branch of the internal carotid was present at all, or 3) the foramen transmitted some other artery entirely, or an unknown vein, or only a carotid nerve, or other nerve, etc. Let us consider these possibilities in reverse order.

Most of the possibilities in category 3 would require hypothesizing something entirely new, for which there is no direct evidence. A unifcrmitarian brand cf parsimony precludes adopting one of these identifications without some more direct evidence. The one possibility of which examples can be provided is that cnly the carotid nerve passed through this foramen, and no artery at all was present. Conroy and Wible (1978) documented the presence of a well defined promontory canal across the ventral surface of the promontorium of Lemur variegatus, but found housed within it only the internal carotid nerve and "no promontory artery" (p. 84) or "only the rudiment of a

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promontory artery" (p. 82). The authors concentrated on the point that it is clearly unsafe to deduce the relative sizes of stapedial versus promontory arteries from the relative sizes of the bony canals presumed to have housed them. However, in their last paragraph, they extrapolate from this to argue that a promontory canal does "not provide unequivocal evidence of...the presence of the promontory artery in fossil forms." It is for this latter point that they have often been cited (e.g. Novacek, 1980: 93), yet this point is not nearly as fundamental as it first appears.

The internal carotid nerve accompanies the internal carotid artery, whether medial or lateral in position (MacPhee, 1981:38, and references cited therein). Therefore the condition Conroy and Wible (1978) observed in Lemur can best be interpreted as homologous to the condition of having a "promontory artery", and within that character, the condition in Lemur is a special case of reduction or loss of the promontory branch specifically. Put another way: it is significant that the condition in Lemur can be shown to be probably one of loss (not primitive absence) of the "promontory artery" on the basis of the position of the internal carotid nerve, and that it is not a case of the promontory canal containing only the nerve while the artery was present but in a medial position. A paleontologist presented with the skull of

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Lemur variegatus would not have made any error of homology, but would only have failed to recognize a more specialized condition within this broader character.

Therefore, the possibility that the internal carotid nerve alone, unaccompanied by the artery, passed through the posterolateral foramen in the nimravid bulla is logically a subset of and included within possibility one above--that a "promontory artery" (an internal carotid in a lateral position) was present.

The second possibility listed above is that this foramen transmitted a stapedial artery--a branch from the internal carotid that passes even farther laterally, through the foramen in the stapes, anteriorly via the inferior ramus to the maxillary artery, and dorsally via the superior ramus, through the tympanic roof to the middle meningeal artery intracranially. Thus the definition of the artery passing through that foramen depends upon its subsequent course; we can only evaluate our identification by the evidence for that subsequent course.

Grooves are present on the ventral surface of the promontorium in some individuals of all nimravid genera. In all but one case, these grooves are in the center of the promontorium and curve anteromedially from the posterolateral foramen toward the internal carotid foramen. In one Hoplophoneus (F:AM 102387), however, a

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well defined groove is present much more laterally, and is aimed directly at the fenestra vestibuli, as if to pass through the stapedial foramen. This specimen of Hoplophoneus has been unlike the other Hoplophoneus in so many features that I might be willing to hypothesize a stapedial artery for just that form and a promontory artery for the other nimravids were it not for the small foramen in the epitympanic recess of Dinictis, Nimravus, and the other Hoplophoneus, as if for a superior ramus of a stapedial artery. Modern carnivorans are all lacking a stapedial artery: in none of them have I found a foramen in this position. (Several mustelids have an anastomosis between the external carotid artery system and the distal stapedial supply to the dura, according to Bugge, 1978, but the foramen for this connection is farther anterior than the nimravid foramen.) Countering the interpretation of that foramen as for a superior ramus of the stapedial is my inability to demonstrate in any specimen a connection between that foramen and the grooves intracranially for the middle meningeal artery.

So the evidence is inconclusive whether this foramen in the bulla is for a stapedial artery. However, if we hypothesize temporarily the presence of a stapedial artery in nimravids, what is the distribution (and polarity) of the feature? The presence of a stapedial artery in the adult is primitive for eutherians: not only is an artery

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piercing the stapes widely present in metatherians but such an artery is also generally present in reptiles as well. I know of no evidence that the stapedial artery was lost in an ancestor common to the Carnivora plus one or more other taxa, so there is no evidence that a stapedial artery within Carnivora would be a reversal (and therefore derived within the group). So if a stapedial is hypothesized, its presence would be a primitive feature for carnivorans and its loss derived within the order.

The first-mentioned possibility remains, however, that the foramen in the bulla transmitted a promontory artery. In the majority of specimens well enough preserved to see the grooves on the ventral face of the promontorium, these grooves run toward the anteromedial corner of the petrosal, beyond which is the internal carotid foramen. Some authors have recognized a distinct, more lateral foramen for the promontory artery to enter the braincase (e.g. Hunt, 1974a). The internal carotid artery, whether in a medial or lateral position, always enters the cranial cavity via the internal carotid foramen. (See the discussion of this foramen in the background section of the morphological description, and in MacPhee, 1981: 40). However, the size or mere presence of an internal carotid foramen cannot be used as evidence for an internal carotid artery: most of the nimravid basicrania show very clear, large channels from the

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anterior opening of the canalis musculotubarius posterodorsally on the epitympanic wing of the sphenoid to the internal carotid foramen. This I interprete as being for an anastomotic branch of the ascending pharyngeal artery (Bugge's (1978) "anastomosis Y"), which could largely or completely replace the internal carotid artery in the adult.

So the evidence for an internal carotid artery is no stronger than that for a stapedial. The evidence that no medially placed branch was present is very strong (see character 22 below), so if any internal carotid artery was present, it was a "promontory artery". Recognizing the weakness of the evidence, what is the polarity of this feature were a promontory artery (=laterally placed internal carotid artery) present in the nimravids?

Evidence for the polarity of the promontory versus medial position of the internal carotid is conflicting. According to Presley (1979), parsimony requires that the primitive pattern of the internal carotid artery within mammals is medial to the tympanic cavity. The cited evidence is the taxonomic distribution of that position: all extant monotremes and marsupials, and some eutherians, have the internal carotid artery "more or less medially placed" (Presley, 1979: 243). The structure of this argument is, of course, out-group comparison since its validity requires that one assume or accept some phylogeny

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within Mammalia that would be contradicted by considering a medial position of more restricted distribution--a synapomorphy. (In this case, the assumptions about groups probably were that monotremes are the sister group of a monophyletic group comprising marsupials and eutherians.)

It is interesting to note, however, that, although Presley built from extensive embryological evidence a very convincing case that the internal carotid at the level of the auditory capsule is a single vessel, he either did not recognize or did not acknowledge the implications of that same embryological evidence for the polarity of this feature. His summary of his observations on a wide range of mammalian embryos (including those of monotremes and Didelphis) included the statement: "In all pre-cartilage stages the vessel [the dorsal aorta = the internal carotid artery] lay in the mesoderm of the roof of the pharynx directly beneath the cochlea" (Presley, 1979: 240). This is the position of a "promontory artery", which then appears to be the most generally distributed state on ontogenetic grounds. If the medial position of the internal carotid in the adult is truly primitive for mammals, the promontory placement that occurs in many eutherians is then a neotenous development (an ad hoc hypothesis) occurring probably more than once within Eutheria. (A further derived condition would arise, of course, if the artery moved during development still

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further lateral relative to the cochlea.) Furthermore, the embryonic placement of the internal carotid artery must be a fetal specialization (also an ad hoc hypothesis). whether for basic mechanical reasons during differentiation, or perhaps for some currently unsuspected adaptational reason, the internal carotid in early stage embryos is in a more lateral position than seen in the ancestral adult--a promontory position--and, in those forms retaining (phylogenetically) the primitive condition as adults, secondarily (ontogenetically) moves medially to that primitive position.

I find the out-group arguments very strong when such large and apparently well defined groups are involved, and therefore am willing to hypothesize that the probable primitive condition within mammals is for the internal carotid artery to be medially positioned in the adult. Many features support the close relationship between metatherians and eutherians relative to monotremes, so that out-group comparison in this case appears to be a stronger source of evidence than does the sequence of states throughout ontogeny. However, in light of the brief embryological data presented by Presley (1979), it must be emphasized that this polarity is not yet conclusively demonstrated. These conclusions could be further tested by examining the development of the internal carotid in reptiles.

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Having concluded that a medially placed, extrabullar internal carotid artery is primitive within Mammalia, the much more difficult questions of the polarities within eutherians and specifically for the Carnivora remain.

Matthew's (1909) reconstruction of the internal carotid circulation for Viverravus hypothesized three branches, a medial carotid, a promontory artery, and a stapedial artery (Figure 51). This reconstruction has been widely adopted as a morphotype from which to derive the carotid patterns in extant eutherians (e.g. Bugge, 1974, 1978; Hunt, 1974; MacIntyre, 1972; Novacek, 1980; and additional references in Presley, 1979). The unquestioned use of this morphotype for nearly three quarters of a century is a good example of the power and persistence of a morphotype once it becomes adopted. In this character, the morphotype gave the ancestral condition and was itself never questioned or tested: both a medial and promontory branch was believed primitive within Eutheria. Thus the morphotype determined the polarity, the ancestral character state, and neither the morphotype nor the conclusions drawn from it in specific analyses were ever directly questioned.

However, three very strong objections to this morphotype can be raised. First, Presley (1979) recently pointed out some fundamental problems with a morphotype containing both a promontory branch and a medial branch.

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Second, I have concluded that Matthew and the majority of subsequent authors have badly misplaced the so-called medial branch in carnivorans and indeed in most eutherians, especially reconstructions of extinct forms, nullifying much of the supposed osteological evidence for a medial branch in these forms. Third, my evaluation of the original evidence for the other two branches, the promontory and the stapedial arteries, leads me to question the validity of the rest of the reconstruction for Viverravus that formed the basis of the morphotype. I will explain each of these three objections in more detail.

Presley (1979) provided embryological information that strongly supports his hypothesis that the medial internal carotid and the lateral internal carotid (the promontory artery) are homologues. They are the same vessel, the developmental equivalent of the dorsal aorta, which has moved either medially or laterally during development (summarized in Figure 52). In addition to the developmental evidence, both Presley (1979) and MacPhee (1981) pointed out additional evidence, such as the association of both vessels with the internal carotid nerve, the entrance of both vessels intracranially to the Circle of Willis via the internal carotid foramen, and the observation that the presence of both vessels in the same mammal has never been demonstrated, only postulated (i.e.,

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this hypothesis of homology has never failed Patterson's (1982) conjunction test).

I have concluded that the main reason a median carotid was included in the morphotype was that extant carnivorans all have a vessel labelled the median carotid artery. As I will explain in more detail in the discussion of character 22, Matthew and all subsequent authors have misplaced the median branch relative to the basicranial bones and the inferior petrosal sinus. If we are parsimoniously uniformitarian, there is actually no evidence whatever for a median branch in Viverravus or any other viverravid or miacid, nor indeed in any of the fossil forms for which three branches have been postulated.

When the remaining evidence is evaluated, the cases for a stapedial artery and a promontory artery are not strong either. I have never been able to find a groove that might reasonably be for a stapedial artery in a miacid or viverravid. I do not seriously question that the presence of a stapedial artery is primitive for eutherians, but this is shown by developmental evidence and out-group comparison: the fossil evidence for a stapedial artery is of dubious value. Grooves are variably present in the center of the ventral surface of the promontorium, but are not as strong evidence for the presence of a promontory position of the artery

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specifically as had previously been thought. This is discussed further under character 19 below.

In sum, not only is the morphotypical use of Matthew's reconstruction of the carotid pattern of Viverravus as a known (unquestioned) eutherian ancestor logically invalid, but the reconstruction itself is based on either extremely tenuous evidence or misconceptions, and not as certain as it was treated by subsequent authors.

The question of the polarity of the promontory artery then remains. An easy answer is not obtainable from the distribution of the feature any more than from the morphotype. Clearly a primitively medial position for therians is indicated by the far medial position in reptiles, monotremes, and marsupials. Within the eutheria, however, a promontory position is fairly common (but by no means universal), occurring especially in groups typically identified as "primitive"--Lipotyphla, Scandentia, Macroscelidia, Primates. This distribution led Archibald (1977) and Wible (1980) to argue that a promontory artery was present in the common ancestor of the Eutheria and therefore primitive within the group for eutherians. I think there are some problems with this conclusion. First the logic of their argument (although never explicitly stated, so my inferences may be wrong) seems to be either a "common is primitive" argument (shown

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invalid in my Methods section above), or an argument that a state occurring in otherwise primitive animals is primitive (also logically invalid in the present system--although perhaps worth exploring in a statistical approach to phylogenetic analysis barely begun to be developed) or an argument that because the promontory artery is present in groups that by themselves form a paraphyletic assemblage--i.e., given the phylogenetic relationships among the orders--the feature must be primitive. The logic of the first two possibilities is invalid, and the third depends on the accuracy of the phylogenetic relationships among the orders of mammals, hardly knowledge of which we are very sure.

I suggest that another possibility should be considered: since the impression that promontory arteries are widespread is based partly on the misapplication of the morphotype to fossils, generating the occurrence in many taxa of supposedly three branches, and by reports for modern taxa based entirely on grooves or dried tissue, and unsubstantiated by direct demonstration of the artery itself, perhaps the presence of the artery in a promontory position is much more restricted in distribution, perhaps a derived feature uniting some subset of the Archonta.

Another question is one of homology. Wible (1980) concluded that all eutherian medial carotids are

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secondarily medial in position, and that their position is therefore not homologous with the medial position primitive for Mammalia. This is an interesting point that I cannot evaluate for any group except Carnivora. In that order, however, I have concluded based on Presley's discussion that the so-called medial internal carotid of carnivorans is a different state than that of other eutherians with a medial artery, because in Carnivora the artery is usually in a tube of rostral entotympanic and thus within the bullar wall for at least part of its route.

In fact, I would hypothesize that a promontory position is primitive within Eutheria, but consider the only valid argument for this to be Presley's embryological data. Although Presley himself did not draw this conclusion, it seems to me that a promontory position is ontogenetically primary, and that subsequent displacement is much less if the adult condition has a promontory artery than if it has a medial artery. Thus the promontory position is the most general, occurring throughout the Eutheria. This hypothesis could be tested by checking the embryological sequence in reptiles and marsupials. I further hypothesize that the strangely intermediate position of the internal carotid artery in Carnivora (see Figure 54), noted by several authors (e.g. Presley, 1979; MacPhee, 1981), is not a "medial internal

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carotid" homologous as a medial carotid with any other in Mammals. Instead it is a synapomorphy of the majority of the Carnivora, a character state derived independently from an ancestral state of a promontory artery. This derived condition of the carotid would exclude the Nimravidae (and perhaps the miacids and viverravids--their condition is not clear) from a close relationship to any subgroup within the Carnivora, though not of course from being sister group to the rest of the order.

It is important to note at this point that these are the same conclusions one reaches if the foramen in the posterior wall of the bulla is hypothesized to be for a stapedial artery rather than a promontory artery. I have therefore considered this feature phylogenetically significant in spite of the uncertainty about the circulatory pattern that was actually present.

16. Expansion of the hypotympanic sinus is frequently accomplished by an invasion by the sinus into the mastoid or squamosal, or both (see extensive review of such cavities and sinuses in Van der Klaauw, 1931: 81-92). No such invasion or epitympanic sinus is evident in the Nimravidae except in Barbourofelis. The latter exhibits an excavation of the posteromedial portion of the mastoid process, partially walled off by an internal crista in the bulla.

The shape of any excavation into the mastoid will be

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a function of the size and shape of the mastoid as well as of the size of the excavation itself and the degree of closure of the entrance to the septum. I see very little difference between the cavity in Barbourofelis and that in Smilodon, for example, except for the more pronounced crista at the entrance in the former. The mastoid sinus, when present in mustelids, is more dorsally positioned because the mastoid itself is enlarged laterally if at all, and not ventrally as in sabertoothed carnivorans. I have not seen the extent of the sinus in mustelids, and therefore do not know well the variation and distribution of this feature. Not only do the differences apparent between the sabertoothed carnivorans' mastoid sinus and the mustelids' argue against their being the same state, but the relationship of this feature to the mastoid suggests that further analysis will depend on a thorough analysis of the different conditions of the whole pars mastoidea of the petrosal.

Out-group comparison generally indicates that such sinuses are derived (but from their widespread distribution within Eutheria, multiply derived if one accepts the broad phylogenetic groupings). It is interesting to note that Hyaenodon crucians has an epitympanic sinus excavated in the mastoid, clearly more dorsal than the sinus in Barbourofelis; a mastoid epitympanic sinus has not been previously reported for

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this genus, to my knowledge. Therefore this is a feature for which the nimravids have a condition primitive for the Carnivora, and for which some other carnivorans indicate a derived condition. There is some evidence from character analysis against considering the mustelid mastoid sinus the same state as that occurring elsewhere, although the more conservative alternative is depicted in Figure 58.

17. Many carnivorans have cristae and struts on the inside of the entotympanic portion of the bulla, usually quite variable in position and degree of development. Nimravids (excluding Barbourofelis) are exceptional among carnivorans in that the internal surface of the ossified portion of the entotympanic is always smooth, without cristae. In this feature, Barbourofelis is much more like other carnivorans in exhibiting several thin cristae perpendicular to the bullar wall. The feloids, canids, procyonids, and ursids have such cristae much less often than the mustelids, and are said by some authors to lack them altogether, although they are in fact occasionally present.

Because of the variability in the size and position of the septa, and the uncertainty about their mode or modes of development, the number of distinct character states present in the Carnivora (or stated in reverse, the level of homology among the conditions observed) is not at all clear. I hypothesized the septum bullae and canid

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septum (discussed under number 11 above) to be derived conditions on the basis of their distinctiveness--i.e. very limited distribution. Until the precise character states are determined for these additional partial septa, if such is even possible, one cannot hypothesize how widely distributed within the Eutheria are the conditions in carnivorans: Van der Klaauw (1931: 214-226) recorded such variable septa and cancellous bone in a great diversity of mammals. I therefore have no hypothesis of polarity for this feature, nor even any certainty that this condition is only one feature.

18. In nimravids (except Barbourofelis), not only is the auditory region increasingly laterally compressed in the more sabertoothed forms, but the petrosals are recessed dorsal to the main level of the basioccipital. The apparent recession is exaggerated by the ventral extension of the mastoid process, the pedestalling of the glenoid, and the vertical flanges on the margins of the basioccipital and basisphenoid. However, in the least modified forms, Dinictis and Nimravus, the petrosals are clearly recessed and the auditory cavity relatively deep, when compared with the auditory cavities of miacids, or any extant carnivoran in which the bulla has been removed. (The extant carnivorans do differ from the miacids in that the mastoid and paroccipital processes of the former are more closely associated with the auditory region and

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usually have facets at least on the dorsal, basal portion of each process where it cups the bulla, even if only slightly.)

As I presently am considering it, the definition of this feature is relatively simple: it is merely the relative level of the promontorium versus the center of the basioccipital (not relative to the flanges). The main question, then, is the polarity of the states of this feature. Marsupials (Didelphis), lipotyphlans (Erinaceus, Sorex), creodonts (Hyaenodon), miacids, and all other carnivorans examined have shallow auditory regions. The distribution of this feature over ontogenetic sequences is not known for taxa with deeply recessed auditory regions, but in other taxa, is shallow from very early stages on (e.g. see Figure 52). Therefore, I conclude that this feature is a specialization of the Nimravidae.

19. The grooves on the ventral surface of the petrosal have been discussed above under number 15, because they are predominantly significant in a reconstruction of the blood vessels and nerves of the region. None in the nimravids, nor indeed in the Carnivora to my knowledge, are closed over tc form canals as are often found in Primates and other archontan groups. The interpretation of the grooves is problematical: Hunt (1974a) found grooves across the promontorium in a variety of carnivoran taxa (e.g., Nandinia, herpestines, Ursus

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americanus, Ailurus, Gulo, otariids, and hyaenids), but subsequent studies of the blood vessels themselves have failed to show any trace of a promontory artery (Bugge, 1978). I consider this more significant than Conroy and Wible's (1978) findings for Lemur (see discussion under number 15), because in the carnivorans, a more medially placed branch is clearly demonstrated (its homologies will be discussed under number 22), so that even if only the internal carotid nerve traveled in the groove on the promontorium, even that would be a major blow to the most recent concepts of the carotid pattern (Presley, 1979) and artery-nerve relationships (MacPhee, 1981). What is more likely is that any of the small nerves or arteries in the ear, like those Story (1951) found in the raccoon and Davis and Story (1943) in the domestic cat, may be causing the small, faint grooves we are seeing on these promontoria, which greatly weakens the usefulness of grooves in deducing the carotid pattern.

It was the presence of such grooves on the promontorium that formed the evidence for Matthew's three branched carotid morphotype (discussed below); I have noted faint grooves in an intermediate position on the promontorium of several miacids, but have never seen one I could identify as a sulcus for a stapedial artery. And of course, there was never any direct evidence for a medial branch of the internal carotid artery in miacids

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comparable to that in the skeleton of extant carnivorans since there have never been bullar elements found in miacids.

I conclude from this analysis that these grooves are not a particularly useful feature in themselves (and have therefore not included them as a separate character in the phylogenetic analysis), and that their interpretation in evaluation of other related features must be done with caution.

20. A well defined deeper pocket was present in the posteromedial portion of the epitympanic recess in Dinictis, Nimravus, and Hoplophoneus. One was not evident in the single skull of Eusmilus available; although the ear region was very compressed and the roof difficult to clean completely, the epitympanic recess is accessible enough that I judge that a typical, well defined secondary pocket to be truly absent in this specimen. The recess itself is a rather odd shape, however, with a much deeper posterior wall than seen in the other nimravids. This I do not judge to be the homologue of the pocket for the posterior crus of the incus because its position and orientation are quite different, compared with the consistency of the position in the other nimravids, and it is not nearly as sharply delimited.

An identical pocket is present in the epitympanic recess of procyonids. (This provides an opportunity to

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test by dissection the identification of this secondary recess as the site of attachment of the ligament to the posterior crus of the incus.) I have not seen this pocket elsewhere, and Brunet (1967) mentioned it only for procyonids. Van der Klaauw (1931) made no mention of it at all. From this limited distribution, I hypothesize that it is a derived feature. I have no relevant ontogenetic information, nor any evidence of structural limitations on this feature. As is the case with many of the characters discussed here, its distribution within the Carnivora should be more thoroughly evaluated.

21. All of the nimravids studied here showed some channel, sulcus, or canal in the anteromedial corner of the auditory region that could be interpreted as a passage for an anastomotic branch of the ascending pharyngeal artery. These channels always ran from some point ventral and anterior towards the internal carotid foramen. The only structure that traverses such a passage in extant carnivorans is the anastomosis between the ascending pharyngeal artery, ventral to the bulla, and the anterior portion of the internal carotid artery, specifically at the loop of the carotid in the internal carotid foramen. The major difference I have noted between the nimravid condition and that of the extant carnivorans with an ascending pharyngeal anastomosis of a significant size is that in nimravids, when the channel is closed over into a

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canal, in some forms this foramen appears to be surrounded by the portion of the basisphenoid produced into a buttress. In extant carnivorans, there is sometimes a foramen in this position, also the end of a dorsally directed channel running to the internal carotid foramen, but because the anteromedial corner of the bulla produces an anteromedial process in place of the basisphenoid buttress seen in nimravids, the foramen in the extant carnivorans is bounded by bulla rather than basisphenoid. Since the difference in bounding elements is clearly related to a consistent difference between nimravids and the extant carnivorans in another feature, and the functional, topological relationships of the foramen or groove remain the same, I do not consider this a particularly strong point refuting the identification of the passage as that for the ascending pharygeal anastomosis. It is interesting to note that Barbourofelis, the one supposed nimravid with an anteromedial process rather than a basisphenoid buttress, also is the one genus to exhibit a ventral-most foramen bounded by bulla rather than basisphenoid.

This anastomosis between the ascending pharyngeal artery and the internal carotid artery is Bugge's (1978) anastomosis Y, which he has demonstrated in a few rodents (Bugge, 1974), and several carnivorans. It was weak and inconsistently present in Procyon and Nasua, and variably

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present in mustelids, most strongly developed in lutrines. I have observed within Lutra always a clear passage for this anastomosis, and sometimes a foramen entirely within the anterior corner of the bulla for the dorsal passage of the vessel to the basisphenoid channel. Bugge (1978: 52) noted an extremely interesting contrast between the herpestids (his "herpestines" since he was recognizing only the family Viverridae for both viverrids and herpestids) and the paradoxurines: the herpestids had a strong anastomosis Y, developed into an arterial rete, whereas the paradoxurines had only a very weakly developed anastomosis if one at all. He reported an anastomosis Y consistently present in hyaenids and felids, but considered it functionally unimportant, in contrast to Davis and Story's (1943) analysis of the domestic cat, in which they considered the ascending pharyngeal artery to have taken over the main intracranial supply. In short, the only carnivorans in which Bugge did not report at least a weak anastomosis Y are ursids and canids, but he considered the anastomosis functionally important only in the herpestids (1978: 59).

If an anteromedial channel is accepted as evidence of an anastomosis from the ascending pharyngeal artery in fossil forms, then the distribution of the anastomosis Y does include the canids and ursids: such a channel is visible in Hesperocyon and Cephalogale. Other authors

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have found the anastomosis in extant Canis and Vulpes as well, ursids, and a large one in Panthera pardus (see review by Cartmill, 1975: 319). This anastomosis, then, is apparently found in most or all of the families of Carnivora, and would therefore seem to be a characteristic of the order at a fairly high level (if the familial groupings are accepted) as Cartmill (1975) inferred. However, the condition in miacids and viverravids is unknown: there is no evidence for the presence of an anastomosis, but since it is possible that the passage was largely bullar and not channelled into the basisphenoid, the lack of a clearly defined sulcus is not conclusive. Bugge (1974) found this anastomosis outside the Carnivora only in a few rodents. Cartmill (1975), in his review of the ascending pharyngeal artery in other mammals, noted the absence of an anastomosis in Rattus, Oryctolagus, and most adult ungulates, but its presence in fetal sheep and adult domestic pig. He also presented convincing arguments that Saban's (1963) anterior carotid artery in cheirogalids and lorises is really an anastomotic branch of the ascending pharyngeal artery.

Both Cartmill (1975) and MacPhee (1981) agreed that the presence of an anastomosis Y in the adult is a derived condition, based primarily on the restricted distribution of the feature: it is apparently a novel feature within eutherians, there occurring in only the few forms

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mentioned above. The ontogenetic evidence is less straightforward. Cartmill (1975: 326) suggested that the anastomosis may be universally present early in development in all mammals, and that retention is derived--i.e. neoteny, an ad hoc hypothesis to accomodate the failure of the ontogenetic evidence to agree with the retained hypothesis of polarity. MacPhee (1981: 40) was more conservative and, while agreeing with the hypothesis that the anastomosis is a derived feature, suggested that the embryological data are too incomplete to require a hypothesis of neoteny.

In either case, the presence of anastomosis Y appears to be a derived character uniting most if not all of the Carnivora (condition in miacids and viverravids unknown). Within the Carnivora, the clearly derived condition is the novel feature in herpestids: the rete described by Bugge (1978) is apparently an autapomorphy for at least part of the family. Since the only occurrence of a derived state of this character within Carnivora is in another family at a finer level of analysis than this one, I have omitted this character from the chart in Figure 58.

22. All previous discussions of the nimravid basicranium have identified a large posteromedial foramen as the posterior carotid foramen, noted that, although posteriorly placed, it is entirely separate from the posterior lacerate foramen, and that the general pattern

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of foramina was rather canoid (large posteriorly placed posterior carotid and large postglenoid foramen). This identification illustrates the outcome of the use of a morphotype at the level of identification of structures, parallel to the use of an ancestral morphotype to assign polarities. In carnivorans, the big foramen at the posteromedial corner of the bulla is the posterior lacerate foramen, any foramen nearby (posteriorly) is the hypoglossal, and one anteriorly and medially, the posterior carotid. This is a morphotype at the level of identification, Level II in Figure 15. It is a usually untested assumption, just as the ancestral morphotype in character 15 was an untested assumption used to assign polarities (Level III). It is worth noting that the use of the ancestral morphotype often caused revision of homologies at Level II so that the interpretation of the morphology corresponded more closely with the morphotype (reciprocal illumination?); in analysis of fossil material especially, in which interpretation is more obviously required even at Level I, in just the determinationcf morphology, a tendency to revise the morphology itself might result from adherence to a morphotype. (This may have been the case in some previous analyses of the septum--see character 11.) But just as a well corroborated ancestral morphotype is often useful if used knowingly, so a homological morphotype is often useful to

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make the process of identification efficient.

Interpretation of nimravid basicrania illustrates some of the inherent dangers. Problems arise when an animal is studied that only superficially fits the morphotype and the identifications are never tested. Any identification of a structure is a hypothesis, not a fact, and should be tested. Omitting Barbourofelis from discussion for the moment, consider the identifications of the foramina in the nimravid basicranium, taking Hough's (1953) discussion as an example. There were hints that some odd features were present: "The basicranial foramina of the Oligocene Felidae are as anomalous as the structureof the auditory region"(p. 99). When a problematic point with the identification appeared, there was a tendency to revise even Level I hypotheses--the 'observed' morphology--to minimize conflict with the morphotypes: "The posterior carotid foramen and the foramen lacerum posterius are separate but they are in the same relative position as in the Canidae and may have been enclosed in a common fossa" (p. 99). Finally, conflicting evidence may be cited but never recognized as a contradiction of the identification: "The carotid canal lies in a distinct groove in the basioccipital extending from the foramen lacerum medium tc the posterior medial corner of the bulla" (p. 103; emphasis mine). (Justice demands a comment about using Hough's work as an example:

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it can be used thus only because she described more fully than was usual both the morphology and her interpretations of it, as well as her phylogenetic conclusions. So, although I disagree with a number of her hypotheses at all levels of analysis, I still find her work among the most useful in some respects because of this relative completeness.)

The result of the unquestioning use of the homological morphotype in the analysis of the nimravid basicranium was that, for over a century, the foramen anteromedial to the posterior lacerate foramen was identified as the posterior carotid and the auditory region was considered canoid. Strong evidence, however, is available that this foramen is instead the petrobasilar foramen, a separate exit of the petrobasilar canal, through which ran the inferior petrosal venous sinus. Given the two competing hypotheses, what is the evidence for each?

Evidence that the medial channel housed the internal carotid artery:

The topological or structural evidence is that underlying the homological morphotype. The well defined opening of the medial channel forms a foramen anterior and medial to the posterior lacerate foramen. It is separated from the posterior lacerate foramen by a bony abutment between the occipital and the entotympanic ventrally and

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the petrosal dorsally. Although the posterior carotid foramen elsewhere in eutherians does not emarginate the basioccipital in the fashion seen here, certainly foramina conveying carotids are bounded by both basioccipital and bulla (such as in herpestids and viverrids).

The comparative evidence that supports the traditional identification is the observation that no recent mammal is known to have a bony separation between the posterior aperture of the petrobasilar canal and the posterior lacerate formen. Also, a medial branch of internal carotid artery is present in almost all other carnivorans, so it was certainly expected in nimravids if they were to fit well within the Carnivora. I do not consider this a valid argument, however, if our goal is to deduce the phylogenetic relationships.

Evidence that the medial channel housed the inferior petrosal sinus:

Topological and structural evidence is found when one looks at the structure and position of features obviously related to the feature being identified, in this case, the channel behind the foramen. A deep, well defined groove in the basioccipital is faced for part of its length by a shallower sulcus in the petrosal, thus forming a petrobasilar canal. There is no channeling in, or anterior to the opening, any enclosure by the entotympanic. The channel is medial to the petrosal,

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between the petrosal and the basioccipital, rather than ventral to the medial rim of the petrosal.

Developmental evidence completely supports the petrobasilar canal identification. In mammalian embryos, the internal carotid is ventral to the petrosal, and stays ventral to at least the medial rim even when it moves to a "medial position" (see Figure 52). The space between basioccipital and petrosal is occupied by veins destined to fuse and form inferior petrosal sinus (Presley, 1979; again see Figure 52).

Finally, the comparative evidence strongly supports this re-identification, but the failure of most paleoanatomists to see that reflects a very widespread misconception about the structure of this region. No recent mammal is known to have the internal carotid artery in a groove or canal in the basioccipital. The artery is always ventral to the petrosal, even if only to the medial-most rim, and only rises dorsally anterior to the petrosal. In extant mammals, if a channel in the basioccipital is present, it is always (to my knowledge) occupied by the inferior petrosal venous sinus.

Extensive confusion about the basic anatomy of the paths of the inferior petrosal venous sinus and the internal carotid artery has resulted both in a number of misstatements about the structures in modern taxa and in numerous reconstructions of fossil taxa which require

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hypothesizing relationships among these structures that never occur in extant animals (a procedure that is usually not parsimonious). In modern mammals with a medial internal carotid, the carotid is ventral to the petrosal, even if only to the medial rim or rostral apex. The promontorium may project below the level of the internal carotid, but the carotid is still ventral to the petrosal until it reaches the internal carotid foramen. At this point, the internal carotid turns dorsally and enters the braincase.

From a ventral aspect when the bulla is intact, the path of the internal carotid first becomes visible in bone at the posterior carotid foramen, either in the bulla or between the bulla and the basioccipital. The artery does not continue dorsally at this point, nor is it "between the petrosal and the basioccipital". It runs anteriorly to the internal carotid foramen, and then turns dorsally. The inferior petrosal venous sinus most often lies in a sulcus on the margins of the dorsal surface of the basioccipital, or if a channel is formed between the basioccipital and petrosal, in that channel. I have found no extant mammal in which the passage of the internal carotid is within this channel, either alone or inside the inferior petrosal sinus.

Ursids present a condition that might be taken at first glance to be an exception to this generalization:

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within the large petrobasilar canal (see Figure 56), the inferior petrosal sinus surrounds a large loop of the internal carotid artery. (This was described in more detail by Hunt, 1977.) The important point is that the path of the internal carotid from its entrance posteriorly into the tympanic region forward to the internal carotid foramen is entirely typical, passing through a tube in the entotympanic portion of the bulla entirely ventral to the petrosal. It is only after entering the cranium through the internal carotid foramen anterior to the petrosal that the carotid turns posteriorly again. The intravenous loop is really a posterior extension of the intracranial portion of the carotid, from within the cavernous sinus.

All published accounts of basicranial anatomy that I have seen fall into two categories: one, in which the author is reporting on paths of blood vessels and nerves based on direct observation of dissected specimens, such as Gray's Anatomy (Williams and Warwick, 1980), Miller et al. (1964), Hunt and Korth (1980), or MacPhee (1981), and two, those in which the author is either explicitly presenting a morphotype drawn from a study of the literature or skeletons and fossils or both, or is reconstructing blood vessels and nerves in individual taxa based on skeletal material, with at most dried tissue if a modern, dermestid-prepared specimen, or, in the case of fossils, often incomplete or distorted specimens. None of

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the published accounts in the first category have ever described an internal carotid artery in the petrobasilar canal or sulcus, either alone or in company with the inferior petrosal sinus. In short, I have never found any account of someone actually seing the internal carotid in that canal. The closest is Presley (1979) who initially defined the medial position as being "in the basicapsular groove or fissure" (p. 238), but by the placement of the vessel in his illustrations implied that his basicapsular groove is the trough or depression ventral tc the petrosal-basioccipital contact, so that the artery is still shown always ventral to the medial rim of the petrosal. When he described the placement of the internal carotid later (p 243), he said that in adults the vessel "may ultimately lie medial to or within the wall of the tympanic cavity", which of course would be ventral to the petrosal.

Matthew (1909: 358) may have started the problem by his reconstruction of Viverravus minutus: "The inner branch of the entocarotid enters between basioccipital and petrosal some distance in front of the foramen lacerum posterius, and presumably passes forward to the foramen lacerum medium as usual among primitive carnivora." As it stands, the description does not make total sense: into where is the artery entering initially? It cannot be intracranially because the vessel still has to pass

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forward to the foramen lacerum medium, which term Matthew was using for the intracranial entrance of the internal carotid artery. So perhaps he meant into a canal, which would be of course in the position of the petrobasilar canal if it is so far dorsal as to be between the basioccipital and petrosal; such a canal in extant forms does not convey the internal carotid.

Whether Matthew was the first to make the error or not, it certainly became embedded in the morphotype taken from his reconstruction of the viverravid and miacid basicranium. For example, Novacek (1980: 50) also stated that "the medial internal carotid artery passed between the petrosal and the basioccipital and basisphenoid bones." Some of the versions of the morphotype have deviated even further from anything observed in extant animals. In Szalay's (1975: 95) eutherian morphotype, for example, the internal carotid was pictured running right next to the inferior petrosal sinus, and was described in the text as "coursing its way between the petrosal and the basiocipital and basisphenoid bones." However, the illustrations shows the inferior petrosal sinus lying extracranially, entering the cranium at the "medial carotid foramen" with the medial carotid artery, and posteriorly entirely distinct from the "foramen lacerum posterior", which is shown giving passage to the "internal jugular vein". This very unusual placement of the

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inferior petrosal venous sinus is not explained in the text.

Even human anatomy, the most well known and best documented, is subject to the same error: MacIntyre (1972: 291) suggested that the "medial branch of the primitive entocarotid artery...may have run concurrently or even coaxially with the inferior petrosal sinus vein (as does the human carotid), but because it could well have followed a separate and more ventral path, that groove may be called the sulcus medialis without prejudice." According to the description of the carotid's path given in Williams and Warwick (1980), the carotid is entirely ventral to and largely anterior to the inferior petrosal sinus, never coaxial with it. There is a plexus of small veins surrounding the artery (p. 686), but the inferior petrosal sinus itself is dorsal, between the basioccipital and petrosal bones (p. 749), and separated by bony partitions from the carotid artery. The artery is partly surrounded by the cavernous venous sinus intracranially, which is the anterior sinus from which the inferior petrosal sinus runs posteriorly, but this is entirely intracranial and quite anterior to the petrosal or its adjacent venous sinus.

The condition of the inferior petrosal sinus in the dog is apparently quite comparable to that in Homo: a small venous sinus lies in the carotid canal, but the

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larger, inferior petrosal venous sinus lies in the petrobasilar canal as is typical in eutherians. Cartmill's (1975: 324) confusion about this condition may have arisen from not realizing that the "ventral petrosal sinus" of Miller et al. (1964) is in an entirely typical channel for the inferior petrosal sinus, and that the "laterally adjacent and parallel carotid canal" is still quite ventral to the medial rim of the petrosal. Of course, the position of the vessels in question and the identity of the surrounding bones provide evidence for the homology of these sinuses, belying Cartmill's statement that "there is presently no evidence".

Figure 53 illustrates two cross sections through a basicranium of Viverra, showing the more ventral position of the carotid canal. It also shows the peculiar position of the so-called medial internal carotid in carnivorans. As discussed by Presley (1979), the carotid in this order is actually in a rather intermediate position, entering the auditory region quite medially, but in many carnivorans, felids and viverrids especially, swinging out laterally, beneath the promontorium. Figure 54 shows this relationship for a canid and a felid, and in comparison, the reconstruction of a nimravid if one hypothesizes an artery in the promontory position. Note that the inferior petrosal sinus is roughly the same in all three; the nimravid has been reconstructed on the basis of the

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re-identification of the large, posteromedial foramen as a petrobasilar foramen.

However, the carotid in extant carnivorans is not a "promontory artery", either, since it is asscciated for most (and frequently all) of its path with the entotympanic, lying in a deep sulcus that is usually closed into a canal anteriorly. Both the lateral curve and the entotympanic tube can be seen in the sectioned Viverra (Figure 53). Elsewhere (character 15), I have considered the passage of the entocarotid within the entotympanic a derived feature uniting the majority of the carnivoran families.

The position of the posterior carotid foramen is frequently taken to be the point at which the carotid enters the cranium itself. Close examination of the skull of Rattus norvegicus, for example, reveals some significant detail, omitted from Greene's (1935: 183) simple statement that "the internal carotid enters the carotid canal between the bulla and the basal plate of the occipital bone to reach the interior of the skull." First, the carotid canal is deeply channeled into the ectotympanic bulla, almost completely enclosed, and there is no corresponding channeling or even emargination on the adjacent basioccipital. Second, although the petrosal is produced so far ventrally that it is clearly visible posteriorly below the level of the basioccipital, the

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carotid canal is always itself ventral to the medial margin of the petrosal. The channel in the medial wall of the bulla runs parallel to the ventral edge of the petrosal, and opens intracranially at the anteromedial apex of the petrosal, the typical position for the internal carotid foramen.

A final example of how widespread taxonomically is this misidentification of the petrobasilar canal can be found in Hunt and Korth's (1980) description of the auditory region of Cynocephalus (Dermoptera): "Medial to the promontorium is a deep channel in the adult...that earlier authors suggested as a possible route for the internal carotid artery in Dermoptera. Dissection of the neonate revealed that this channel houses only the inferior petrosal venous sinus, its bony wall formed by bulla, petrosal, and occipital."

The conclusion must be that the best identification of the medial canal and foramen in nimravids, based on the anatomy of extant eutherians, is as a petrobasilar canal and foramen that provided passage for the inferior petrosal venous sinus. It appears to be unique for the canal to exit via a foramen separated from the posterior lacerate foramen by a bony abutment between the basioccipital and the entotympanic ventrally and petrosal dorsally. The separate exit of the sinus itself is rather common: confluence with the sigmoid sinus can be either

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intra- or extracranial. But the bony abutment ventrally between the entotympanic and occipital defining this separation osteologically is to my knowledge an entirely novel condition, another autapomorphy for the Nimravidae.

23. Apparently accompanying the bony separation in nimravids of the petrobasilar foramen from the posterior lacerate foramen is the placement of the latter farther laterally than is typical for extant carnivorans. This feature is considered here as a separate character because this lateral position occurs in the absence of any bony separation of the petrobasilar foramen in miacids and viverravids, paleonyctid and hyaenodontid creodonts (as noted by Matthew, 1909: 358), and in a great variety of other mammals. In many mammals, such as marsupials and lipotyphlans, the medial margins of the basioccipital are oblique, so that the basioccipital narrows anteriorly and is much broader posteriorly, pushing the posterior lacerate foramina laterally as a result. But as shown by the photo of Lemur in Cartmill (1975: 326), for example, in which these margins are oblique, the posterior lacerate foramen is still more laterally placed than required merely by the slope of the basioccipital.

I have not done a thorough survey of this feature in the Mammalia, nor can I find any discussion of this character elsewhere in the literature. However, my tentative hypothesis is that the more medial position of

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the posterior lacerate foramen, at the posteromedial corner of the bulla, is a novel feature occurring in all carnivorans except miacids, nimravids, and viverravids: I have not yet found it elsewhere within the Mammalia. I have no ontogenetic information relevant to this feature, nor do I see any structural constraints except that imposed by the shape of the basioccipital.

This discussion of the posterior lacerate foramen might be an appropriate context to mention that a much more frequently cited character is the degree of confluence of this foramen with the hypoglossal foramen. Feloids are often said to have such confluence, and canids or caniforms to lack it. Clark and Guensburg (1972) reviewed the inconstancy of this feature, and pointed out that a lack of confluence is primitive and therefore not canoid, and that the feature is largely uninformative.

24. A postglenoid foramen is primitively present in eutherians for the exit of the superior petrosal venous sinus, part of the external jugular drainage. I know of no alternative identification of a foramen in this position, and therefore no disagreement about the character states involved.

The wide distribution of the postglenoid foramen throughout the Mammalia, including within the Carnivora, argues that its presence is primitive for the order, and its reduction or loss derived within the order. Its

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presence in all nimravids except Barbourofelis is therefore not directly phylcgenetically informative, but is indirectly informative: the reduction or loss of the postglenoid foramen in the feloid Carnivora is another derived feature excluding the Nimravidae from membership within that group.

Barbourofelis's lack of a postglenoid foramen is hypothesized to be derived, but no details are apparent to indicate whether or not it is derived in common with any other losses within Carnivora. Certainly, ad hoc hypotheses of convergence are usually adopted for the reduction or loss of the postglenoid foramina in the aquatic carnivorans--phocids, otariids, and lutrines.

Conroy (1980) made the interesting suggestion that the orientation of the transverse sinus, as a function of relative cerebral expansion, is the factor determining the presence or absence of a contribution from a superior petrosal sinus (his petrosquamosal sinus) to the external jugular drainage. "Naturally the orientation of the transverse sinus is dependent to a large degree upon the growth of the cerebral hemispheres, and in catarrhines it normally comes to lie more horizontally after complete cerebral growth. In most mammals without a caudally expanded cerebral cortex, the transverse sinus retains the more vertical position relative tc the skull base and consequently the petrosquamcus sinus remains as a large

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channel which empties via the postglenoid foramen into the external jugular system (Butler, 1967). By the 18-26 mm embryonic stage an important crossroad is reached in mammalian development whereby the relative caudal expansion of the cerebral cortex will determine whether the internal or external jugular system will be the dominant channel of intracranial venous drainage."

The variation with the Carnivora offers a test of this hypothesis. Comparisons of Figures 25 and 44 show that there is little difference between the canid and felid in the angle of the tentorium, and therefore of the transverse sinus it contains. Yet the canid retains a large superior petrosal sinus draining through a large postglenoid foramen and the felid lacks this drainage entirely. Indeed the distribution of the reduction or loss of the postglenoid foramen is not obviously correlated either with a particular morphological development, nor with any single ecological generalization: in the aeluroids, the postglenoid foramen is reduced or missing, in the terrestrial arctoids, it is large and implies a large intracranial contribution to the external jugular system, and in the aquatic arctoids, it is again reduced or missing.

25. Characterizing a three-dimensional shape is often difficult to do unequivocally; certainly identifying the square or rectangular cross section and blunt ends of

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the nimravid mastoid process is simple enough within a genus, or even for Dinictis and Nimravus together, but more difficult beyond that. The more extremely saber-toothed forms have proportionally much larger mastoid processes, keeping pace with the increased pedestalling of the glenoid fossa. Even in these, however, I think I see a squarer cross-section and blunter, more defined end, than can be seen in Smilodon for example.

I have not found this condition of the mastoid process in any other carnivoran (although I say this with some hesitation because the mastoid process in ursids certainly comes close), nor in any other mammal (although here again I must qualify this by pointing out that I have not done what I consider to be a very wide or thorough survey). But as a temporary hypothesis, subject to future test, I have considered the condition in nimravids, including Barbourofelis, to be an autapomorphy.

One related feature for which I did not have sufficient information, but which should be considered in future studies, is the composition of the mastoid process. The degree to which the squamosal contributes is evidently variable and may be of taxonomic significance. For example, Segall (1943) notes that the mastoid process in canids if formed by the pars mastoidea of the periotic alone, whereas in procyonids, the squamosal bears a

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"post-tympanic process", which forms the anterior paart of the mastoid process. It was difficult to tell in many cases, but all nimravids for which I could determine this feature had a mastoid process formed by both squamosal and the pars mastoidea.

A related feature was described by Cifelli (1982: 802): "The tympanohyal, the most cranial element of the hyoid bar (Van der Klaauw, 1931), fuses in most mammals to the mastoid portion of the petrosal, forming the processus hyoideus. In primitive carnivorans (Viverravus, Vulpavus, Didymictis), however, the tympanohyal is fused to a ventromedial prolongation of the squamosal, which arches over the facial nerve and contacts the promontorium. This unusual condition may be synapomorphous for the Carnivora at a fairly high level." Here again is an example of conflicting hypotheses at a very low level in the analysis: I have carefully examined the same specimens studied by Cifelli and see no evidence whatever of a squamosal contribution to the processus hyoideus. (The most proximal hyoid element in carnivorans may probably be safely assumed to be the tympanohyal, as was assumed by Cifelli for miacids, in contrast to other orders in which the tympanohyal and perhaps even stylohyal form the processus hyoideus by co-ossifying with the skull. However, it is important to realize that we have no direct evidence supporting this assumption for miacids.) In

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every case, the articular facet for the most proximal hyoid element is on a process from the anteromedial corner of the pars mastoidea of the petrosal. A secondary consideration is whether it would be reasonable to identify the condition Cifelli described as a synapomorphy for the order even if it were observed in two or three genera of miacids or viverravids, since it has never been found in any extant carnivoran (in which the condition can be more easily determined, in juveniles) nor in any fossil representative of either feliforms or caniforms. But the question of the feature's polarity is, of course, quite secondary to the question of whether the feature even occurs in any taxon.

26. A broad shelf or crest connects the paroccipital and mastoid processes in all known miacids and viverravids, in creodonts, in various other potential out-groups such as Pantolestes, and to varying degrees within the extant Carnivora--ursids, otariids, and some mustelids. I am not satisfied with the definition of the states of this character: I think at least two phenomena are involved. One is the degree to which the paroccipital process is broadly separated from the auditory region and projects posteriorly, forming a broad, leaf-like shape. The other is the degree to which the mastoid bone is produced into a connecting shelf between the mastoid and paroccipital processes. Clearly the latter condition will

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be influenced by the size of the paroccipital process itself.

Testing whether this feature is a complex or not, and if it is, sorting out the various states, will require a more complete analysis of the diversity within the order than I was able to do for this study. As an initial hypothesis, therefore, I will consider it one feature, and base the polarity on the condition in out-groups to the Carnivora. The nimravid conditon (for those nimravids retaining paroccipital processes) is thus considered primitive.

27. A widely recognized derived feature in feloids is the degree to which the paroccipital process becomes broad and closely cups the posterior wall of the bulla. This might reasonably be considered part of the previous character, and is certainly related to the orientation and size of the paroccipital process discussed above. Again, the nimravid condition is that one primitive for the order, so listing it separately until re-analysis of the posterolateral corner of the auditory region is a conservative approach that will not bias the analysis of the phylogenetic relationships of the nimravids.

28. The buttress formed by the basisphenoid against the anteromedial corner of the bulla has been described above for every nimravid except Barbourofelis. In the

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latter, a typical carnivoran anteromedial process may be found. The size of this process differs widely among the Carnivora; its distribution outside the order is largely unknown to me and apparently undocumented in the literature. I have no confidence that all the extensions of the anteromedial corner are homologous to one another, but insufficient evidence is available to evaluate the question. Neither do I have any ontogenetic or structural information relevant to the homologies of the basisphenoid buttress. Therefore, I very tentatively hypothesize an autapomorphy for the Nimravidae.

29. The margins of all nimravid basioccipitals examined here, except those of Barbourofelis, were produced into ventrally directed flanges on the medial margins of the auditory bullae. Although these flanges do unquestionably increase the perception of lateral compression of the median flooring bones, especially in Hoplophoneus, the two features are at least somewhat independent of each other. One of the most laterally compressed interbullar distances can be found in Barbourofelis, which stands in sharp contrast to the other nimravids in having extensive bullar-basioccipital contact, but directed the opposite way: the basisphenoid dorsally overlaps the bulla broadly (see Figure 41).

Huge ventral flanges occur elsewhere in ursids and otariids. These flanges look quite different in that they

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are thicker at the base and rounded at the tips, so the homology is not very certain and would ideally be tested eventually by checking the developmental timing and mechanisms of the two types of flanges. Certainly the restriction of these flanges to a few families within the Carnivora argues that it is a novel feature within the Mammalia, and therefore derived. It has been tentatively hypothesized to be derived for the phylogenetic summary present here.

30. Ossification ventrally of the tentorium, anterior to the petrosal, is found in the feloid carnivorans, and no where else within the order (see Figure 55). More extensive ossification is considered derived on ontogenetic grounds, which would support its polarity based on its distribution among out-groups such as Liptyphla. However, elsewhere in the Mammalia, ungulates also have a well cssified tentorium. This raises the interesting possibility that ossification of the tentorium might be a synapomorphy for a ferungulate group, and the reduction in ossification of the tentorium a reversal that would be derived for the nimravids and caniforms. The next step would clearly be a comparison of the details of the tentoria of carnivorans and ungulates.

31. A well defined petrobasilar sulcus is present in all carnivorans I have examined thus far (e.g., Viverra in

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Figure 53). The caniforms and nimravids have the additional development of some degree of flange from the basioccipital roofing this sulcus and a corresponding deepening of the lateral portion of the sulcus in the margin of the petrosal, forming an enclosed petrobasilar canal. This is shown in intracranial view in Figure 57 and in cross section in Figure 56. The latter includes for comparison the cross section diagrammed by Van Kampen (1905: 597), illustrating the extent to which the size and definition of the petrobasilar canal has been overlooked in carnivorans.

Marsupials and lipotyphlans have only very shallow sulci if any for the inferior petrosal venous sinus. The condition in miacids, viverravids, and creodonts is uncertain because of a lack of suitably prepared material. The petrobasilar sulcus or canal is not discussed particularly in the literature (indeed the intracranial morphology in general of eutherians seems to have been largely ignored), so I am not at all sure of this feature's distribution within the Eutheria. However, from a very incomplete sampling of ungulates, in addition to those groups mentioned above, I hypothesize that the roofing of the sulcus to form a petrobasilar canal is a derived feature within the Carnivora.

32 and 33. The presence or absence of the various foramina from the venous channels on the inside of the

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squamosal bone to the exterior of the skull has not been noted in mammals (except for the condition of the postglenoid foramen) since the one thorough survey paper of Cope (1890). He did not discuss any variation in placement of the foramina, and thus did not evaluate explicitly any potential indications that more than one character state might be involved.

The mastoid and postparietal foramina are rare in metatherians, but some supposedly comparable foramina occasionally occur. They are certainly of wide distribution within the eutherians, so if their presence is not primitive for the group Eutheria, it is very likely primitive within the subclass. The majority of the Carnivora are lacking all foramina, or all except the postglenoid foramen. Cope reports a mastoid foramen in only Ursus and Arctotherium of the carnivorans he surveyed, and Hyaenodon within the creodonts, but missed its presence in Dinictis and other nimravids (except Barbourofelis). I cannot determine with certainty its condition in miacids or viverravids because the skulls are generally crushed.

The loss of the mastoid foramen within an eutherian order would be derived as evaluated here, and if treated as a synapomorphy, would unite all Carnivora excluding ursids and nimravids. This latter hypothesis is not particularly testable at the character analysis level,

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however, because two or more occurrences of a loss of a feature are not likely to have accompanying information relevant to an evaluation of whether the losses are homologous.

Similarly, the postparietal foramen is present in ursids, creodonts, nimravids, and although doubtful again, probably miacids and viverravids. The same caveat applies to the loss of this feature in the remaining Carnivora. Because of the lack of testability at the character analysis level, I have omitted both of these features from the cladogram in Figure 58.

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PHYLOGENETIC CONCLUSIONS

From each of the character analyses, the phylogenetic implications of the distribution of the character may now be extracted. Here again a tabulation will be most informative. Each feature observed in nimravids will fall into one of the following categories:

1) a specialization of the nimravids not found in other Carnivora; i.e., a hypothesized autapomorphy for the family Nimravidae (and therefore a hypothesized synapomorphy for the members of that family).
2) a feature that, like (1), is derived relative to the condition hypothesized to have occurred in the common ancestor of the Carnivora, and therefore of limited distribution within the order, but one not unique to nimravids--i.e., a hypothesized synapomorphy for the Nimravidae and some other taxon or taxa within the order.
3) a feature that is hypothesized to be the same state as that in the common ancestor of the Carnivora, and thus is a more generally distributed character in which is included one (or more) less general characters; i.e., the nimravid character state is primitive relative to a synapomorphy hypothesized to unite two or more other taxa within the order.
4) uninformative characters, which may be so for a variety of reasons:

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a) no hypothesis of polarity: I was unable to decide which was the more general condition of which the other was a modification, or

b) the feature is primitive for Carnivora and I have no information about modifications of the feature within the order, or

c) the character was not well enough defined for me to have confidence that I knew which occurrences in different taxa were the same state and which were different, or

d) repetitions: after analysis, the feature seemed to me to be part of another character already included in one of the first three, informative categories.

As was outlined in the summaries, analysis of Barbourofelis produced incongruities in many character distributions if that genus was included in the Nimravidae. Therefore I will continue to consider it separately so the evidence for its phylogenetic relationships can be assessed directly. In the following lists and discussion, "nimravid" is restricted to the nimravines and hoplophonines, excluding Barbourofelis. The condition in Barbourofelis is indicated separately to the left of each character.

1. Seven characters are hypothesized to be autapomorphies for the family Nimravidae. (Character

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numbers as in the summary. "+" preceeding the character number indicates that Barbourofelis also possesses the derived condition seen in nimravids, "-" that it does not, and "?" that the state cannct be determined. For details in each case, see the individual taxonomic descriptions and the character analysis.)

? 1. flattened or gently curved (vertical), platelike ectotympanic

\+ 3. external auditory meatus wider than the tympanic notch; faces into base of postglenoid process

\- 13. entotympanic a thick "sandwich", constructed of very thin outer layers of bone with a thick layer inside of cancellous bone

\- 18. auditory region is recessed, lying well dorsal to the level of basisphenoid/basioccipital

\- 22. presence of a separate posterior petrobasilar foramen: a bony partition separates the exit of inferior petrosal sinus from posterior lacerate foramen

\+ 25. mastoid processes square or rectangular in cross section, with blunt ends

\- 28. basisphenoid forms a buttress against anteromedial corner of bulla; anteromedial process from bulla never present

2. Five features in nimravids were derived relative to the primitive condition within Carnivora, and were also

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shared with other taxa, and are therefore potential synapomorphies. However, there was no clear pattern emerging from these five characters, and there were characters uniting groups among the other carnivorans excluding the nimravids, so that the most parsimonious arrangement is that shown in Figure 58, in spite of these five characters. (Symbols preceeding the numbers indicated derived condition present or absent in Barbourofelis as above.)

? 5. anterior crus of ectotympanic broadened, horizontal, nearly meeting posterior crus, forming a closed or nearly closed ring

===> shared with hyaenids, herpestids, canids, mustelids, and some felids

\+ 7. processus tubarius from anterior crus of ectotympanic present, appressed to tympanic roof, between fossa muscularis major and epitympanic recess.

===> shared with canids and procyonids

\- 20. secondary deep pocket in epitympanic recess

===> shared with procyonids

\- 29. margins of basioccipital produced into vertical flanges that extend ventrally against the medial side of each bulla.

===> shared with ursids and otariids

\- 31. horizontal flange of basioccipital at least partly

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roofing the inferior petrosal sulcus, together with medial margin of petrosal forming the petrobasilar canal

===> shared with all extant caniform families and the Viverridae

3. Ten features of nimravids are hypothesized to be primitive within the Carnivora, but exhibit derived states in some other members of the order, which thereby define groups from within which the Nimravidae are excluded. (In the following summary, an '*' preceeding the character number indicates that Barbourofelis possesses the derived condition, unlike the other nimravids, where a "-" that Barbourofelis' condition is the same as the primitive one in nimravids, which of course is no evidence of closeness of relationship, and "0" flags those features that Barbourofelis cannot have because of some structural impossibility.)

- 9. osseous canalis musculotubarius is a complete tube of ectotympanic

===> unites extant arctoid families

0 11. septum bullae from ectotympanic plus entotympanic (or one modified by loss of the entotympanic contribution as perhaps is the case in hyaenids), or a partial entotympanic septum from the dorsal edge of the caudal entotympanic.

===> first condition unites four extant feloid families,

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excluding Nimravidae; second is an autapomorphy for Canidae (condition not known in miacidae and viverravidae)

* 12. a completely ossified bulla, in extant carnivorans from the ossification of two or more entotympanics; (contributing elements not determinable in Barbourofelis and many other extinct taxa)

===> unites all extant families of carnivorans, excluding the Nimravidae (condition not known in miacids and viverravids)

\- 15. more medial position of internal carotid artery and its capture in a tube in rostral entotympanic (often reduced to groove if artery reduced)

===> unites all extant families of carnivorans, excluding the Nimravidae (condition not known in miacids and viverravids)

(If the posterior carotid foramen in nimravids is instead identified as a foramen for a persistent stapedial artery, then the absence of a stapedial artery in the extant families is a synapomorphy excluding the nimravids, so the significance of the character remains the same.)

* 16. invasion of mastoid by the hypotympanic sinus

===> occurs in hyaenids, some mustelids, Barbourofelis, and Smilodon

\- 23. posterior lacerate foramen located medially, at posteromedial corner of bulla

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===> a feature of all families of extant carnivorans

* 24. reduction or loss of postglenoid foramen

===> unites four extant families of feloids excluding the Nimravidae; convergent in aquatic arctoids

26. reduction or loss of the broad shelf connecting mastoid and paroccipital processes

===> unites four extant families of feloids, excluding the Nimravidae; occurs also in the Canidae and in some arctoids

0 27. paroccipital processes cup the posterior margin of bulla

===> unites four extant families of feloids, excluding the Nimravidae

* 30. tentorium is well ossified ventrally, overlying the anterolateral face of the petrosal

===> unites the four extant families of feloids, excluding the Nimravidae (condition not known in miacids and viverravids)

The remaining characters were considered uninformative for one or more of the reasons listed above. Reasons for that decision are given for each character in the individual analyses. Recognized distributions of the informative characters are summarized in Figure 58.

A variety of synapomorphies can be seen to unite the feloid carnivorans excluding the nimravids, thus contradicting Martin's (1980) phylogenetic hypothesis.

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Some of the characters he cited to define a family Felidae separate from the Nimravidae, are actually feloid characters and unite several families while excluding the Nimravidae. There were no characters that indicated that the nimravids might be sister group to the feloids as a whole, and a couple of characters united caniforms and feliforms excluding the nimravids, so position 2 on the phylogeny in Figure 7 was also contradicted.

There were no characters that demonstrated a relationship between the Nimravidae and the Canidae specifically, but one can hardly say that Hough's hypothesis was contradicted because she was trying to argue for a relationship between the entire Felidae, including the Nimravinae and excluding those taxa she placed in a Machairodontidae (see Table 1), and the Canidae; that set of relationships is thoroughly contradicted by the seven autapomorphies for the Nimravidae as here constituted.

Nor was specific support found for Flynn and Galiano's hypothesis that the Nimravidae are sister group to the Caniformia: although the derived characters listed in category two above are shared most often with one or more caniform family, there emerged no pattern of character distribution that would allow for a parsimonious placement of the Nimravidae either most closely related to or within the Caniformia. The various derived characters

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uniting subgroups within the Caniformia and not present in Nimravidae preclude that, as do the two synapomorphies for the Carnivora as a whole excluding the Nimravidae. Therefore, the most parsimonious phylogenetic hypothesis is that shown in Figure 58, in which the Nimravidae is the sister group to the rest of the Carnivora. This placement is reflected in the classification (p. 18) in which the Nimravidae is placed as a plesion family in the Carnivora but outside Yither suborder.

The final problem is the relationship of Barbourofelis to the nimravids or elsewhere. I found only two (or three if you wish to count character 7 in Figure 58 as well) derived characters of the nimravids that Barbourofelis had as well. In contrast, Barbourofelis did not possess the remaining seven restricted autapomorphies for the Nimravidae. Thus, based on the basicranium, if Barbourofelis is retained within the Nimravidae, it would be sister group to the rest of the nimravids. This is evidence that Barbourofelis is presenting a problem but not that Barbourofelis does not actually belong within the family. The only proper refutation of that hypothesis would be a better supported hypothesis--and I have no better evidence linking Barbourofelis anywhere else. Two characters unite it with the feloids, and one specifically with the hyaenids (although a very weak one--the invasion of the mastoid by the hypotympanic sinus). But this is

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about the same weight of evidence uniting Barbourofelis with the nimravids, and Barbourofelis is also lacking many synapomorphies that unite the felcids excluding it.

Clearly Barbourofelis shares one spectacular character or character complex with a subset of the nimravids: it possesses very long saber-like canines and the exaggerated cranial morphology that accompanies such hypertrophy of the canines, but superficially this genus shares the same features with a subset of the felids as well. My conclusion is that the phylogenetic position of Barbourofelis is presently very poorly supported, but that I can offer no stronger hypothesis. Until I can, I leave this genus in the Nimravidae, but with the caveat that its relationships need further study. To this end, a detailed study of Eusmilus, Hoplophoneus, and Sansanosmilus would probably be extremely informative.

In conclusion, the basicranial anatomy of the Nimravidae indicates a phylogeny in which the family arose independently of the rest of the Carnivora from the common ancestor to the order (with the possibility that some taxa we are now placing in Miacidae or Viverravidae are also likely to form sister group(s) to the rest of the Carnivora, including perhaps the Nimravidae). This evidence should be considered as well as dental and other cranial features when the relationships of the family are evaluated. No claim is made that the basicranium is a

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source of any more reliable characters than anywhere else in the animal, only that the complexity of the basicranium is likely to provide a wealth of features to consider. I would still recommend that any morphological analysis be performed and reported in a more explicit fashion than is the current practice, since the topology of the phylogeny is a direct function of the character analysis if some sort of standardized cladistic analysis is adopted for deriving that phylogeny.

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Adams, George I. 1896. The extinct Felidae of North America. American Journal of Science 1:419-444.

Albercht, Pere. 1980. Ontogenesis and morphological diversification. Amer. Zool. 20:653-667.

Albercht, Pere, Stephen Jay Gould, George F. Oster, and David B. Wake. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5(3):296-317.

Archibald, J. David. 1977. Ectotympanic bone and internal carotid circulation of eutherians in reference to anthropoid origins. J. Human Evol. 6:609-622.

Arnold, E. N. 1981. Estimating phylogenies at low taxonomic levels. Zeitschrift für zoologische Systematik und Evolutionsforschung 19(1):1-35.

Baskin, Jon A. 1981. Barbourofelis (Nimravidae) and Nimravides (Felidae), with a description of two new species from the late Miocene of Florida. J. Mammalogy 62(1):122-139.

Bast, Theodore H. and Barry J. Anson. 1949. The Temporal Bone and the Ear. Springfield, Illinois: Charles C. Thomas. xviii + 478 pp.

Beaumont, Gérard de. 1964. Remarques sur la classification des Felidae. Eclogae geol. Helv. 57(2):837-845.

Beer, G. R. de. 1937. The Development of the Vertebrate Skull. Oxford: Clarendon Press. 552 pp.

Bock, Walter J. 1973. Philosophical foundations of classical evolutionary classification. Systematic Zoology 22(4):375-392.

Bock, Walter J. 1977. Foundations and methods of evolutionary classification. pp. 851-895 in Hecht, M. K., P. C. Goody, and B. M. Hecht, eds., Major Patterns in Vertebrate Evolution. New York: Plenum Press.

Bock, Walter J. and Gerd von Wahlert. 1965. Adaptation and the form-function complex. Evolution 19(3):269-299.

Booth, Ernest S. 1948. Laboratory Anatomy of the Cat. Dubuque, Iowa: Wm. C. Brown. 59 pp.

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Bradley, O. Charnock, and Tom Grahame. 1943. Topographical Anatomy of the Dog. Edinburgh, Scotland: Oliver and Boyd. xii + 316.

Brunet, Michel. 1967. Contribution à la connaissance des genres Dinictis et Hoplophoneus (Carnivora--Felidae). Travaux de l'Institut de Géologie et d'Anthropologie Préhistorique de la Faculté des Sciences de Poitiers 8:1-37, plus 28 figures and 6 plates.

Bugge, J. 1974. The cephalic arterial system in insectivores, primates, rodents and lagomorphs, with special reference to the systematic classification. Acta Anatomica 87(Suppl. 62):1-96.

Bugge, J. 1978. The cephalic arterial system in carnivores, with special reference to the systematic classification. Acta Anatomica 101:45-61.

Cartmill, M. 1975. Strepsirhine basicranial structures and the affinities of the Cheirogaleidae. p. 313-354 in Luckett, W. P. and F. S. Szalay, eds., Phylogeny of the Primates. New York: Plenum Press.

Cartmill, M. 1981. Hypothesis testing and phylogenetic reconstruction. Zeitschrift für zoologische Systematik und Evolutionsforschung 19(2):73-96.

Cartmill, M. and R. D. E. MacPhee. 1980. Tupaiid affinities: the evidence of the carotid arteries and cranial skeleton. p. 95-132 in Luckett, W. P., ed., New York: Plenum Press.

Cifelli, R. L. 1982. The petrosal structure of Hyposodus with respect to that of some other ungulates, and its phylogenetic implications. J. Paleon. 56(3):795-805.

Clark, John and Thomas E. Guensburg. 1972. Arctoid genetic characters as related to the genus Parictis. Fieldiana: Geology 26(1):1-76.

Conroy, Glenn C. 1980. Evolutionary significance of cerebral venous patterns in paleoprimatology. Z. Morph. Anthrop. 71(2):125-134.

Coombs, Margery C. and Walter P. Coombs, Jr. 1982. Anatomy of the ear region of four Eocene artiodactyls: Gobiohyus, ?Helohyus, Diacodexis and Homacodon. J. Vert. Paleo. 2(2):219-236.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Cooper, Gale and Alan L. Schiller. 1975. Anatomy of the Guinea Pig. Cambridge, Massachusetts: Harvard University Press. 417 pp.

Cope, Edward. D. 1880a. On the extinct cats of America. Amer. Natur. 14(12):833-858.

Cope, Edward D. 1880b. On the genera of the Creodonta. Proc. Amer. Phil. Soc. Proc. (1882) 19:76-82.

Cope, Edward Drinker. 1882. On the systematic relations of the Carnivora Fissipedia. Proc. Amer. Philos. Soc. 20:471-475.

Cope, Edward D. 1884. The Creodonta. Amer. Natur. (1884):255-267, 344-353, 478-485.

Cope, Edward D. 1890. On the foramina perforating the posterior part of the squamosal bone of the Mammalia. Proc. Amer. Philos. Soc. (1890):452-461.

Crisci, Jorge V. 1982. Parsimony in evolutionary theory: law or methodological prescription? J. theor. Biol. 97:35-41.

Crisci, J. V., and T. F. Stuessy. 1980. Determining primitive character states for phylogenetic reconstruction. Syst. Botany 5(2):112-135.

Crouch, James E. 1969. Text-Atlas of Cat Anatomy. Philadelphia: Lea and Febiger. xvi + 399 pp.

Cunningham, Daniel John, and G. J. Romanes. 1972. Cunningham's Textbook of Anatomy. London: Oxford University Press. xv + 996 pp.

Davis, D. Dwight and H. Elizabeth Story. 1943. The carotid circulation in the domestic cat. Zoological Series, Field Museum of Natural History. 28(1):1-47.

Dover, Gabriel. 1982a. A molecular drive through evolution. Bioscience 32(6):526-533.

Dover, Gabriel. 1982b. Molecular drive: a cohesive mode of species evolution. Nature 299:111-117.

Eisenberg, John F. 1981. The Mammalian Radiations: an analysis of trends in evolution, adaptation, and behavior. Chicago: University of Chicago Press. xx + 610 pp.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Eldredge, N. and J. Cracraft. 1980. Phylogenetic Patterns and the Evolutionary Process: Method and theory in comparative biology. New York: Columbia University Press. viii + 349 pp.

Estabrook, George F. 1977. Does common equal primitive? Systematic Botany 2(1):36-42.

Farris, James S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18(4):374-385.

Field, Hazel E. and Mary E. Taylor. 1950. An Atlas of Cat Anatomy. Chicago: University of Chicago Press, 75 pp.

Fisher, Ronald A. 1958. The Genetical Theory of Natural Selection. New York: Dover. xiv + 291 pp.

Fleischer, Gerald. 1978. Evolutionary Principles of the Mammalian Middle Ear. Berlin: Springer-Verlag. 70 pp.

Flower, W. H. 1869. On the value of the characters of the base of the cranium in the classification of the Order Carnivora, and on the systematic position of Bassaris and other disputed forms. Prcc. Zool. Soc. London 1869:4-37.

Flynn, John J. and Henry Galiano. 1982. Phylogeny of Early Tertiary Carnivora, with a description of a new species of Protictis from the middle Eocene of northwestern Wyoming. Amer. Mus. Novitates no. 2725, 64 pp.

Fortey, R. A. and R. P. S. Jeffries. 1982. Fossil and phylogeny--a compromise approach. pp. 197-234 in Joysey, K. A. and A. E. Friday, eds., Problems of Phylogenetic Reconstruction. Systematics Association Special Volume No. 21. New York: Academic.

Foulds, L. R., M. D. Hendy, and David Penny. 1979. A graph theoretic approach to the development of minimal phylogenetic trees. J. Molecular Evolution 13:127-149.

Gaffney, E. S. 1979. An introduction to the logic of phylogeny reconstruction. p. 79-111 in Cracraft, J. and N. Eldredge, eds., Phylogenetic Analysis and Paleontology. New York: Columbia University Press.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Gardner, Ernest, Donald J. Gray, and Rónan O'Rahilly. 1960. Anatomy: a regional study of human structure. Philadelphia: Saunders. 999 pp.

Getty, R., H. L. Foust, E. T. Presley, and M. E. Miller. 1956. Macroscopic anatomy of the ear of the dog. Amer. J. Vet. Res. 17:364-375.

Ghiselin, Michael T. 1966. An application of the theory of definitions to systematic principles. Systematic Zoology 15(2):127-130.

Ghiselin, Michael T. 1980. Phylogenetic mythogenesis and paleontology. Evolution 34(4):822-824.

Ginsburg, L. 1961. La faune des carnivores Miocenes de Sansan (Gers). Memoires Mus. National d'Hist. Natur. ns, series C, 9:1-190.

Ginsburg, L. 1979. Révision taxonomique des Nimravini (Carnivora Felidae) de l'Oligocène des Phosphorites du Quercy. Bull. Mus. natn. Hist. nat., Paris, 4th series, section C, 1(1):35-49.

Gould, Stephen Jay. 1977. Ontogeny and Phylogeny. Cambridge, MA: Belknap, Harvard Univ. Press. ix + 501 pp.

Greene, Eunice C. 1935. Anatomy of the rat. Trans. Amer. Phil. Soc., n.s. 27:1-370.

Guth, Christian. 1964. Sinus veineux et veines de l'arrière-crane de quelques carnivores fossiles. Annales de Paléontologie (Vertébrés) 50(1):33-43.

Hecht, Max K. 1976. Phylogenetic inference and methodology as applied to the vertebrate record. pp. 335-363 in Hecht, M. K., W. C. Steere and B. Wallace, eds., Evolutionary Biology Vol. 9. New York: Plenum.

Hecht, M. K. and J. L. Edwards. 1976. The determination of parallel or monophyletic relationships: the proteid salamanders--a test case. Amer. Naturalist 110:653-677.

Hecht, M. K. and J. L. Edwards. 1977. The methodology of phylogenetic inference above the species level. pp. 3-51 in Hecht, M. K., P. C. Goody, and B. M. Hecht, eds., Major Patterns in Vertebrate Evolution. New York: Plenum Press.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Hough, Jean. 1944. The auditory region in some Miocene carnivores. J. Paleontol. 18:470-479.

Hough, Jean. 1948. The auditory region in some members of the Procyonidae, Canidae, and Ursidae: its significance in the phylogeny of the Carnivora. Bull. Amer. Mus. Nat. Hist. 92:67-118.

Hough, Jean. 1953. Auditory region in North American fossil Felidae: its significance in phylogeny. Geol. Surv. Prof. Pap. 243-G:95-115.

Hunt, Robert M., Jr. 1974a. The auditory bulla in Carnivora: an anatomical basis for reappraisal of carnivore evolution. J. Morph. 143(1):21-76.

Hunt, Robert M., Jr. 1974b. Daphoenictis, a cat-like carnivore (Mammalia, Amphicyonidae) from the Oligocene of North America. J. Paleont. 48(5):1030-1047.

Hunt, Robert M., Jr. 1977. Basicranial anatomy of Cynelos Jourdan (Mammalia: Carnivora), an Aquitanian amphicyonid from the Allier Basin, France. J. Paleont. 51(4):826-843.

Hunt, Robert M., Jr. and William W. Korth. 1980. The auditory region of Dermoptera: morphology and function relative to other living mammals. J. Morph. 164:167-211.

Jamieson, E. B. 1946. Illustrations of Regional Anatomy. Section II: Head and Neck. 6th ed. Edinburgh, Scotland: E. and S. Livingstone. iv + 64 pp.

Jannett, Frederick J., Jr. 1975. "Hip glands" of Microtus pennsylvanicus and M. longicaudus (Rodentia: Muridae), voles without hip glands. Systematic Zoology 24(2):171-175.

Jardine, N. 1969. The observational and theoretical components of homology: a study based on the morphology of the dermal skull-roofs of rhipidistian fishes. Biol. J. Linn. Soc. 1:327-361.

Jollie, Malcolm. 1962. Chordate Morphology. Huntington, NY: Krieger (reprint with corrections, 1972). xiv + 478 pp.

Jong, R. de. 1980. Some tools for evolutionary and phylogenetic studies. Zeitschrift für zoologische Systematik und Evolutionsforschung 18(1):1-23.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Kluge, Arnold G. 1971. Concepts and principles of morphological and functional studies. pp. 3-41 in Waterman, Allyn J. ed., Chordate Structure and Function. New York: Macmillan.

Kluge, Arnold G. 1976. Phylogenetic relationships in the lizard family Pygopodidae: an evaluation of theory, methods and data. Misc. Pub. Mus. Zool. Univ. Michigan no. 152, 72 pp.

Kluge, Arnold G. 1977. Concepts and principles of morphologic and functional studies. pp. 1-27 in Kluge, A. G., ed., Chordate Structure and Function, 2nd ed., New York: Macmillan.

Kluge, Arnold G. and James S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Systematic Zoology 18:1-32.

Kollar, E. J. and C. Fisher. 1980. Tooth induction in chick epithelium: expression of quiescent genes for enamel synthesis. Science 207:993-995.

Kuhn, Thomas S. 1970. The Structure of Scientific Revolutions, 2nd ed. Chicago: Univ. Chicago Press. xii + 210 pp.

Lakatos, Imre. 1970. Falsification and the methodology of scientific research programmes. pp. 91-196 in Lakatos, I. and A. Musgrave, eds., Criticism and the Growth of Knowledge. London: Cambridge Univ. Press.

Leidy, Joseph. 1869. The extinct mammalian fauna of Dakota and Nebraska. Journal Academy of Natural Sciences of Philadelphia 7:1-472.

Leidy, Joseph. 1871. Report on the vertebrate fossils of the Tertiary formations of the west (4th annual report of the USGS, for 1870). Part 4, no. 4, special reports. pp. 340-370 in F. V. Hayden, ed. Preliminary report of the United States Geological Survey of Wyoming and portions of contiguous territories. U. S. Govt. Printing Office. 511 pp.

Luckett, W. Patrick and Wolfgang Maier. 1982. Development of deciduous and permanent dentition in Tarsius and its phylogenetic significance. Folia Primatologica 37:1-36.

MacIntyre, Giles T. 1972. The trisulcate petrosal pattern of mammals. pp. 275-303 in Dobzhansky, T., M. K. Hecht, and W. C. Steere, eds., Evolutionary

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Biology vol. 6. New York: Appleton-Century-Crofts.

MacPhee, R. D. E. 1977. Ontogeny of the ectotympanic-petrosal plate relationship in strepsirhine prosimians. Folia Primatologica 27:245-283.

MacPhee, R. D. E. 1979. Entotympanics, ontogeny and primates. Folia Primatologica 31:23-47.

MacPhee, R. D. E. 1981. Auditory regions of primates and eutherian insectivores: morphology, ontogeny, and character analysis. Contributions to Primatology vol. 18, xv + 282 pp.

Martin, L. D. 1980. Functional morphology and the evolution of cats. Trans. Nebraska Acad. Sci. 8:141-154.

Marx, H. and G. B. Rabb. 1970. Character analysis: an empirical approach applied to advanced snakes. J. Zool., London 151:525-548.

Matthew, W. D. 1909. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. Memoirs Amer. Mus. Nat. Hist. 9(6):291-567.

Matthew, W. D. 1910. The phylogeny of the Felidae. Bull. Amer. Mus. Nat. Hist. 28:289-316.

Mayr, Ernst. 1969. Principles of Systematic Zoology. New York: McGraw-Hill. xi + 428 pp.

Mayr, Ernst. 1974. Cladistic analysis or cladistic classification? Zeitschrift für zoologische Systematik und Evolutionsforschung 12:94-128.

McDowell, S. B. 1958. The Greater Antillean insectivores. Bull. Amer. Mus. Nat. Hist. 115:113-214.

Merriam, John C. and Chester Stock. 1932. The Felidae of Rancho La Brea. Carnegie Institution of Washington, pub. no 422. xvi + 231 pp.

Mickevich, M. F. 1981. Quantitative phylogenetic biogeography. pp. 209-222 in Funk, V. A. and D. R. Brooks, eds., Advances in Cladistics. Bronx: New York Botanical Garden.

Miller, M. E., G. C. Christensen, and H. E. Evans. 1964. Anatomy of the Dog. Philadelphia: W. B. Saunders.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

941 pp.

Mitchel, Edward and Richard H. Tedford. 1973. The Enaliarctinae: a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. Bull. Amer. Mus. Nat. Hist. 151(3):201-284.

Mivart, St. George. 1881. The Cat: an introduction to the study of backboned animals especially mammals. London: John Murray. xxiii + 557 pp.

Moore, W. J. 1981. The Mammalian Skull. Cambridge, UK: Cambridge University Press. xi + 369 pp.

Neff, Nancy A. 1982. The Big Cats: The Paintings of Guy Coheleach. New York: Abrams. 244 pp.

Nelson, Gareth J. 1973. The higher-level phylogeny of vertebrates. Systematic Zoology 22(1):87-91.

Nelson, Gareth J. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. Systematic Zoology 27(3):324-345.

Nelson, Gareth J. and Norman Platnick. 1981. Systematics and Biogeography: Cladistics and Vicariance. New York: Columbia Univ. Press.

Novacek, M. J. 1977. Aspects of the problem of variation, origin and evolution of the eutherian auditory bulla. Mammal Rev. 7(3&4):131-149.

Novacek, M. J. 1980. Cranioskeletal features in tupaiids and selected Eutheria as phylogenetic evidence. pp. 35-93 in Luckett, W. P., ed., New York: Plenum Press.

Owen, Richard. 1847. Report on the archetype and homologies of the vertebrate skeleton. Report 16th Meeting British Assoc. Advancement of Science 1846:169-340.

Patterson, Colin. 1977a. Cartilage bones, dermal bones and membrane bones, or the exoskeleton verus the endoskeleton. pp. 77-121 in Andrews, S. Mahala, R. S. Miles, and A. D. Walker, eds., Problems in Vertebrate Evolution. Linnean Society Symposium Series no. 4. London: Academic Press.

Patterson, Colin. 1977b. The contribution of paleontology to teleostean phylogeny. pp. 579-643.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

in Hecht, M. K., P. C. Goody, and B. M. Hecht, eds., Major Patterns in Vertebrate Evolution. New York: Plenum Press.

Patterson, Colin, 1982. Morphological characters and homology. pp. 21-74 in Joysey, K. A. and A. E. Friday, eds. Problems of Phylogenetic Reconstruction. Systematics Association Special Volume No. 21.

Piveteau, J. 1931. Les chats des Phosphorites du Quercy. Annales de Paleontologie 20:107-152.

Piveteau, J. 1961. Mammifères: Origine Reptilienne, Évolution: Carnivora. Traité de Paléontologie Tome VI(Volume 1):641-820.

Pocock, R. I. 1916a. On the course of the internal carotid artery and the foramina connected therewith in the skulls of the Felidae and Viverridae. Ann. Mag. Nat. Hist. series 8. 17:261-269.

Pocock, R. I. 1916b. The tympanic bulla in hyaenas. Proc. Zool. Soc., London. 1916:303-307.

Pomel, Auguste. 1853. Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique superieur de la Loire, et surtout dans la vallée de son affluent principal, l'Allier. Paris: J.-B. Baillière. 193 pp.

Presley, R. 1979. The primitive course of the internal carotid artery in mammals. Acta Anatomica 103:238-244.

Raup, David M. 1979. Biases in the fossil record of species and genera. pp. 85-91. in Schwartz, J. H. and H. B. Rollins, eds., Models and Methodologies in Evolutionary Theory. Bull. Carnegie Museum of Natural History no. 13.

Reighard, Jacob, H. S. Jennings, and Rush Elliott. 1935. Anatomy of the Cat. New York: Holt, Rinehart and Winston. 486 + 99 pp.

Repenning, Charles A. and Richard H. Tedford. 1977. Otarioid seals of the Neogene. Geological Survey Prof. Paper 992:vi + 93, and 24 plates.

Saban, R. 1963. Contribution à l'étude de l'os temporal des Primates. Description chez l'Homme et les Prosimiens. Anatomie comparée et phylogénie.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Mémoires du Muséum National d'Histoire Naturelle, série A, Zoologie. 29:1-378.

Schaeffer, Bobb, Max K. Hecht, and Niles Eldredge. 1972. Phylogeny and paleontology. pp. 31-46 in Dobzhansky, T., M. K. Hecht, and W. C. Steere, eds., Evolutionary Biology vol. 6. New York: Appleton-Century-Crofts.

Schlosser, Max. 1888. Die Affen, Lemure, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des Europäischen Tertiärs und deren beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten. II Theil. Beiträge zur Paläeontologie Österreich-Ungarns. 7(1):225-386.

Scott, W. B. 1889. Notes on the osteology and systematic position of Dinictis felina, Leidy. Proc. Acad. Nat. Sci. Philadelphia 41:211-244.

Scott, W. B. and G. L. Jepsen. 1941. The mammalian fauna of the White River Oligocene. Part 1: Insectivora and Carnivora. Trans. Amer. Phil. Soc. ns 28:1-153.

Segall, Walter. 1943. The auditory region of the arctoid carnivores. Field Mus. Nat. Hist. Zool. Ser. 29:33-59.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist. 85:xvi + 350.

Simpson, G. G. 1953. The Major Features of Evolution. New York: Columbia Univ. Press. xx + 434 pp.

Simpson, G. G. 1961. Principles of Animal Taxonomy. New York: Columbia Univ. Press. xii + 247 pp.

Simpson, G. G. 1975. Recent advances in methods of phylogenetic inference. pp. 3-19 in Luckett, W. P. and F. S. Szalay, eds., Phylogeny of the Primates. New York: Plenum Press.

Sisson, Septimus. 1914. The Anatomy of the Domestic Animals. 2nd Edition. Philadelphia: Saunders. 930 pp.

Smith, G. R. and R. K. Koehn. 1971. Phenetic and cladistic studies of biochemical and morphological characteristics of Catostomus. Systematic Zoology

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

20(3):282-297.

Sneath, Peter H. A. and Robert R. Sokal. 1973. Numerical Taxonomy: the Principles and Practice of Numerical Classification. San Francisco: W. H. Freeman. xv + 573 pp.

Solounias, Nikos. 1981. The Turolian fauna from the island of Samos, Greece: with special emphasis on the hyaenids and the bovids. Contrib. to Vert. Evol. 6:xvi+ 232 pp.

Starck, Dietrich. 1967. Le crane des Mammifères. pp. 405-549 in Grassé, Pierre-P., ed. Traité de Zoologie: Anatomie, Systématique, Biologie. Tome 16. Mammifères: Téguments et Squelette. Paris: Masson et Cie.

Stevens, P. F. 1980. Evolutionary polarity of character states. Ann. Rev. Ecol. Systematics 11:333-358.

Story, H. Elizabeth. 1951. The carotid arteries in the Procyonidae. Fieldiana: Zoology 32(8):475-557.

Swindler, Daris R. and Charles D. Wood. 1973. An Atlas of Primate Gross Anatomy: Baboon, Chimpanzee, and Man. Seattle: University of Washington Press. xiii + 370 pp.

Szalay, Frederick S. 1975. Phylogeny of primate higher taxa. pp. 91-125 in Luckett, W. P. and F. S. Szalay, eds., Phylogeny of the Primates. New York: Plenum Press.

Tandler, J. 1906. Zur Entwickelungsgeschichte der arteriellen Wundernetze. Anat. Hefte 31:237-265.

Tedford, Richard H. 1976. Relationship of pinnipeds to other carnivores (Mammalia). Systematic Zoology 25(4):363-374.

Tedford, Richard H. 1978. History of dogs and cats: a view from the fossil record. In Nutrition and management of dogs and cats, part M23. St. Louis: Ralston Purina Co.

Teilhard de Chardin, P. 1945. Les Felides de Chine: Premiere Partie. Les formes fossiles. Publications de l'Institut de Geobiologie no. 11:1-35.

Thenius, Erich. 1967. Zur Phylogenie der Feliden (Carnivora, Mamm.). Z. zool. Syst. Evol. 5:129-143.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Turner, H. N. 1848. Observations relating to some of the foramina at the base of the skull in Mammalia, and on the classification of the Order Carnivora. Proc. Zool. Soc., London. 1848:63-88.

Van der Klaauw, C. J. 1931. The auditory bulla in some fossil mammals. Bull. Amer. Mus. Nat. Hist. 52:1-352.

Van Kampen, P. N. 1905. Die Tympanalgegend des Säugetierschädels. Morphologische Jahrbuch 34:321-722.

Walker, Warren F. 1980. Vertebrate Dissection, 6th edition. Philadelphia: Saunders. xvii + 425 pp.

Wessells, Norman K. and Elizabeth M. Center, eds. 1975. Vertebrates: a laboratory test. Los Altos, CA: William Kaufmann. 238 pp.

Wible, John R. 1980. The primitive course of the mammalian internal carotid artery. (abstract).Amer. J. Phys. Anthrop. 52:292-293.

Wiley, E. O. 1981. Phylogenetics: the Thecry and Practice of Phylogenetic Systematics. New York: Wiley. xv + 439 pp.

Williams, Peter L. and Roger Warwick. 1980. Gray's Anatomy, 36th British Ed. Philadelphia: W. B. Saunders. 1578 pp.

Wincza, H. 1896. Über einige Entwickelungsveränderungen in der Gegen des Schädelgrundes bei den Säugethieren.
look it up. Bulletin International de l'Académie des Sciences de Cracovie 1896(7):326:337.

Wortman, J. L. 1892. The ancestry of the Felidae. pp. 94-101 in H. F. Osborn and J. L. Wortman. Fossil mammals of the Wahsatch and Wind River Beds. Collection of 1891. Bull. Amer. Mus. Nat. Hist. 4:81-147.

Zangerl, Rainer. 1948. The methods of comparative anatomy and its contribution to the study of evolution. Evolution 2:351-374.

Zhanxiang, Qiu, and Norbert Schmidt-Kittler. 1982. On the phylogeny and zoogeography of the leptarctines (Carnivora, Mammalia). Paläont. Z. 56(1/2):131-145.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Zittel, Karl A. 1893. Handbuch der Palaeontologie. Palaeozoologie. IV Band: Vertebrata (Mammalia). xi + 799 pp.

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Table 1: Classification of the Carnivora presented by Hough in her 1953 study of the felid auditory region. Her group Machairodontoidea was based on various features all reflecting the sabertoothed morphology of its members. The characters that formed the basis for the Cyno-feloidea can be simply summarized as a canoid basicranial morphology.

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MACHAIRODONTOIDEA

HOPLOPHONEIDAE
Hoplophoneus

EUSMILIDAE
Eusmilus
Barbourofelis

MACHAIRODONTIDAE
Smilodon

CYNO-FELOIDEA

CANIDAE

FELIDAE
NIMRAVINAE
Dinictis
Nimravus

FELINAE
Felis, etc.

AELUROIDEA (HERPESTOIDEA)

DAPHOENIDAE
VIVERRIDAE
?HYAENIDAE

ARCTOIDEA

PROCYONIDAE
URSIDAE
?MUSTELIDAE

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Table 2: A list of the fossil material studied in detail in this analysis. Given for each specimen is the current identification (according to the housing institution), the specimen number (one preceeding asterisk denotes the type of the species, two asterisks the type of the genus and species), and the specimen's approximate age, in North American Land Mammal Ages and their equivalent in Lyellian epochs.

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FOSSIL MATERIAL STUDIED

name	specimen no.	age
NIMRAVIDAE		
Barbourofelis morrisi Schultz, Schultz, and Martin left temporal region and occiput	F:AM 61961	late Clarendonian (=late Miocene)
Barbourofelis morrisi skull	F:AM 61871	late Clarendonian (=late Miocene)
Barbourofelis morrisi skull	F:AM 61876	late Clarendonian (=late Miocene)
Barbourofelis morrisi occiput and part of right temporal region	F:AM 61891	late Clarendonian (=late Miocene)
Barbourofelis morrisi skull, juvenile	F:AM 61895	late Clarendonian (=late Miocene)
Barbourofelis lovei Baskin posterior part of cranium	UF 23796	late Clarendonian (=late Miocene)
Barbourofelis lovei left temporal region	UF 24432	late Clarendonian (=late Miocene)
Barbourofelis lovei posterior two-thirds of skull	UF 36867	late Clarendonian (=late Miocene)
Dinictis felina Leidy skull	**AMNH 455	Orellan (=middle Oligocene)
Dinictis cylops Cope skull	*AMNH 6937	Early Arikareean (=late Oligocene)
Dinictis squalidens Cope skull	AMNH 8777	Orellan (=middle Oligocene)
Dinictis sp. skull	F:AM 62034	Orellan (=middle Oligocene)
Dinictis sp. skull	F:AM 104823	Orellan (=middle Oligocene)

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Dinictis sp. left and part of right temporal regions	AMNH (S.D. 230-4152)	Orellan (=middle Oligocene)
Dinictis felina Leidy skull	ANSP 12547	Orellan (=middle Oligocene)
Dinictis felina Leidy skull of subadult	USNM 15889	Orellan (=middle Oligocene)
Dinictis sp. portion of posterior half of skull	YPM 20268	Orellan (=middle Oligocene)
Eusmilus cerebralis Cope skull	*AMNH 6941	Early Arikareean (=late Oligocene)
Hoplophoneus primaevus Leidy skull	AMNH 1406	Orellan (=middle Oligocene)
Hoplophoneus sp. skull	F:AM 62022	Orellan (=middle Oligocene)
Hoplophoneus sp. skull	F:AM 62078	Chadronian (=middle Oligocene)
Hoplophoneus sp. skull	F:AM 69417	Chadronian (=middle Oligocene)
Hoplophoneus sp. posterior half of skull, frontal plane section	AMNH 82440	Orellan (=middle Oligocene)
Nimravus brachyops Cope skull	AMNH 6930	Early Arikareean (=late Oligocene)
Nimravus brachyops skull	AMNH 6931	Early Arikareean (=late Oligocene)
Nimravus sp. skull	F:AM 62020	Whitneyan (=late Oligocene)
Nimravus sp. skull, juvenile	F:AM 99259	Early Arikareean (=late Oligocene)
Nimravus sp. skull	YPM 14385	Early Arikareean (=late Oligocene)

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FELIDAE

Pseudaelurus sinclairi Matthew skull	F:AM 61835	early Barstovian (=middle Miocene)
Smilodon floridanus left temporal region, transversely sectioned	LACM HC6997	Rancholabrean (=Pleistocene)
Smilodon floridanus anterior portion of right temporal region, transversely sectioned	LACM HC6998	Rancholabrean (=Pleistocene)
Smilodon floridanus longitudinal (sagittal) section of right temporal region	LACM HC6999	Rancholabrean (=Pleistocene)
Smilodon floridanus sphenoid and both temporal regions of a subadult	LACM HC7000	Rancholabrean (=Pleistocene)
Smilodon floridanus portion of left and right mastoid and ecto- and entotympanics, and part of a petrosal	LACM HC7001	Rancholabrean (=Pleistocene)

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Table 3: Taxa represented by specimens used in this study for comparison. Age and provenance are given for fossil material.

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MARSUPIALIA

Paramelidae

Parameles sp.

Didelphidae

Didelphis virginianum

LIPOTYPHLA

Erinaceidae

Erinaceus europaeus

Echinosorex gymnurus

CREODONTA

Hyaenodontidae

Hyaenodon crucians--Oligocene, North America

Paleonyctidae

Proviverra rapax--Eocene, North America

Thinocyon velox--Eocene, North America

CARNIVORA

incertae sedis, *Paleogale lagophagus*--Oligocene, North America

Miacidae

Vulpavus sp.--Eocene, North America

Viverravidae

Viverravus spp.--Eocene, North America

Viverridae

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Paradoxurinae

Paradoxurus .sp--juvenile

Paguma .sp--young adult

Arctictis sp.

Nandinia binotata--juveniles and adult

Viverrinae

Genetta sp.

Viverricula sp.--juvenile

Civettictis sp.

Viverra zibetheca

Cryptoproctinae

Cryptoprocta ferox--juvenile and adult

Felidae

Felinae

Felis spp.

Neofelis nebulosa

Pantherinae

Panthera spp.--juveniles and adults

Acinonycinae

Uncia uncia

Acinonyx jubatus--juvenile and adults

Acinonyx trumani--Pleistocene, North America

Herpestidae

Hemigalinae

Eupleres goudoti

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Hemigalus hardwickei

Herpestinae

Herpestes aurcpunctatus--juvenile and adult

Bdeogale sp.

Xenogale sp.

Galidiinae

Galidia elegans

Hyaenidae

Protelinae

Proteles cristatus--juvenile and adult

Hyaeninae

Hyaena hyaena

Crocuta crocuta--juvenile and adult

Canidae

Caninae

Canis latrans

Hesperocyoninae

Hesperocyon sp.--Oligocene, North America

Ursidae

Ursinae

Ursus americanus--juveniles and adult

Hemicyoninae

Cephalogale gracilis--Oligocene, Europe

Procyonidae

Procyoninae

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Nasua nasua--juvenile and adult

Procyon lotor

Mustelidae

Lutrinae

Lutra spp.--juvenile and adult

Taxidiinae

Taxidea spp.

Melinae

Meles sp.--juvenile and adult

Mustelinae

Mustela sp.

Mephitinae

Mephitis sp.

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Table 4: An outline of character and cladistic analyses summarizing the analysis at each step, characterizing the hypothesis resulting from each step, and listing ad hoc hypotheses invoked at each step in response to contradictions in the evidence. The steps and levels correspond to those in Figure 15.

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CHARACTER ANALYSIS

	ad hoc hypotheses denying information from a lower level of the analysis
STEP 1:	
clustering individual morphologies into the smallest consistent cluster (character state) and then identifying features, i.e., clustering states into inclusive sets of homologues.	contra level I individual variation environmental influence breakage or incomplete preservation

HYPOTHESIS.--feature X in taxon A is the same as feature X in taxon B.

STEP 2:	
constructing a hierarchy of characters, each of which comprises comparable character states, based on the relative generality of the characters	contra level II loss neoteny incompleteness of fossil record

HYPOTHESIS.--feature Y is more general than, and includes, the more specialized feature Z.

CLADISTIC ANALYSIS

STEP 3:	
finding the cladogram that best accounts for all the character distributions	contra level II convergence reversal neoteny incompleteness of fossil record
HYPOTHESIS.--taxon A is more closely related to B than either is to C.	contra level III reordering of character states

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Table 5: Three simple examples of possible conflict between evidence for polarity from the distribution cf character states across adult morphologies and across ontogenetic stages. See text for discussion.

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A.	mysticetes	odontocetes
adult:	no teeth	teeth
fetal:	teeth	teeth

	state considered primitive	ad hoc hypothesis
novelty:	no teeth	LCSS
ontogeny:	teeth	

B.	other chordates	humans
adult:	small brain	large brain
fetal:	large brain	large brain

	state considered primitive	ad hoc hypothesis
novelty*:	small brain	
ontogeny:	large brain	NEOTENY

*and transformationist assumptions. see text.

C.	other Ambystoma	axclotl
adult:	no gills	gills
juvenile:	gills	gills

	state considered primitive	ad hoc hypothesis
novelty:	no gills	
ontogeny:	gills	NEOTENY
cladistic position:	no gills	

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Table 6: A summary of the characters of the ear region most comprehensively discussed in the literature, in the context of which to consider the summary of nimravid structure that is drawn from the descriptions in this study. One can quickly see the coherence of Flower's Aeluroidea, and, although less immediately, of his Arctoidea as well. Nandinia is omitted from the summaries for Viverridae, and Potos from Procyonidae, because both are so anomalous in so many ways that current concepts of the basic morphology of the families would be obscured. The families are designated by single letters, as follows:

F = Felidae	U = Ursidae
Y = Hyaenidae	O = Otariidae
V = Viverridae	R = Procyonidae
H = Herpestidae	M = Mustelidae
C = Canidae	P = Phocidae

The symbols have the following meanings:

+	feature is present or condition is true
-	feature is absent or condition is not true
x	condition is variable within the family
0	not applicable (i.e. structure missing)
?	no information in this literature

Sources:

Bugge, 1978; Clark and Guensburg, 1972; Flower, 1869; Davis and Story, 1943; Hunt, 1974; Mivart, 1885; Repenning and Tedford, 1973; Segall, 1943; Turner, 1848; Zhanxiang and Schmidt-Kittler, 1982.

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ARTERIAL

	F	Y	V	H	C	U	O	R	M	P
anastomosis (a4 intracranial, a2 extracranial) between ext. carotid a. (int. maxillary a.) and arterial circle (int. carotid a.), thru sphenorbital foramen	+	+	+	+	+	-	?	x	x	?
a4 developed into at least simple rete (intracranial)	+	+	+	?	-	-	?	-	-	?
rete in a4 large; rete in a2 present	+	+	-	-	-	-	?	-	-	?
loops of int. carotid a. within cavernous venous sinus or inferior petrosal sinus	-	-	-	-	-	+	?	-	-	?
internal carotid artery:	F	Y	V	H	C	U	O	R	M	P
at least somewhat reduced	+	+	+	?	-	-	-	-	-	-
very reduced or absent	+	+	-	-	-	-	-	-	-	-
anastomosis X present, between occipital a. and vertebral a.	+	+	+	+	+	-	?	-	+	?
anastomosis Y present, between ascending pharyngeal a. and distal int. carotid a. at int. carotid for.	+	-	-	+	+	-	?	x	x	?

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arterial supply to dura annexed by ext. carotid a. system:	F	Y	V	H	C	U	O	R	M	P
via distal stapedial a. stem and proximal supraorbital a.	+	+	+	-	+	+	?	+	x	?
via distal supraorbital branch from orbital arteries	-	-	-	+	-	-	?	-	x	?

AUDITORY BULLA

external auditory meatus:	F	Y	V	H	C	U	O	R	M	P
at least a short tube	-	+	-	+	x	+	+	+	+	+
a long tube (at least ventral lip)	-	-	-	-	-	+	+	+	+	+

external auditory meatus directed:	F	Y	V	H	C	U	O	R	M	P
laterally	0	+	0	+	+	-	-	+	-	0
anterolaterally	0	-	0	-	-	+	+	-	+	0

septa:	F	Y	V	H	C	U	O	R	M	P
bilaminar septum bullae	+	-	+	+	-	-	-	-	-	-
?unilaminar ?ectotympanic septum	-	+	-	-	-	-	-	-	-	-
partial, anterior, entotympanic septum	-	-	-	-	+	-	x	x	x	x
posterior, entotympanic septa	-	-	-	-	+	-	-	-	+	-

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condition of caudal entotympanic:	F	Y	V	H	C	U	O	R	M	P
elongate E1 (Hunt's designation)	-	?	-	-	-	+	+	-	x	-
hemispherical E1	+	-	+	+	-	-	-	x	-	-
?no separate E1 & E2 (could be an elongate E1 fused early to E2)	-	?	-	-	+	-	-	x	x	+

caudal entotympanic small relative	F	Y	V	H	C	U	O	R	M	P
to rostral entotym. & ectotym.	-	?	-	-	-	+	+	-	x	-
caudal entotympanic expanded	+	-	+	+	+	-	-	+	x	+

auditory cavity expanded	F	Y	V	H	C	U	O	R	M	P
posterior to promontorium	+	+	+	+	+	-	-	+	+	+

	F	Y	V	H	C	U	O	R	M	P
greatly expanded ectotympanic	-	+	-	-	-	-	-	-	-	-

tympanic cavity expanded into	F	Y	V	H	C	U	O	R	M	P
excavation in adjacent mastoid	-	+	-	-	-	-	-	-	x	-

	F	Y	V	H	C	U	O	R	M	P
hypomeatal sinus present	-	-	-	-	-	+	+	-	-	-

carotid canal complete tube for	F	Y	V	H	C	U	O	R	M	P
some portion of its length	x	0	x	+	+	+	+	+	+	+

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relative length of carotid canal:	F	Y	V	H	C	U	O	R	M	P
full length of bulla	-	0	-	-	-	+	+	-	x	-
intermediate	+	0	-	+	-	-	-	+	x	+
very short, anteriorly placed	-	0	+	-	+	-	-	-	-	-

anteromedial apex of bulla overlaps	F	Y	V	H	C	U	O	R	M	P
internal carotid foramen	+	+	+	-	+	x	+	-	-	+

	F	Y	V	H	C	U	O	R	M	P
epitympanic sinus present	-	-	-	-	-	-	?	+	+	?

suprameatal fossa excavated into	F	Y	V	H	C	U	O	R	M	P
squamosal (further modified in M)	-	-	-	-	-	x	-	+	x	?

SURROUNDING STRUCTURES

expanded paroccipital process	F	Y	V	H	C	U	O	R	M	P
cupping posterior portion of bulla	+	+	+	+	-	-	-	-	-	-

part of mastoid process from	F	Y	V	H	C	U	O	R	M	P
squamosal	?	?	?	?	-	+	?	+	+	?

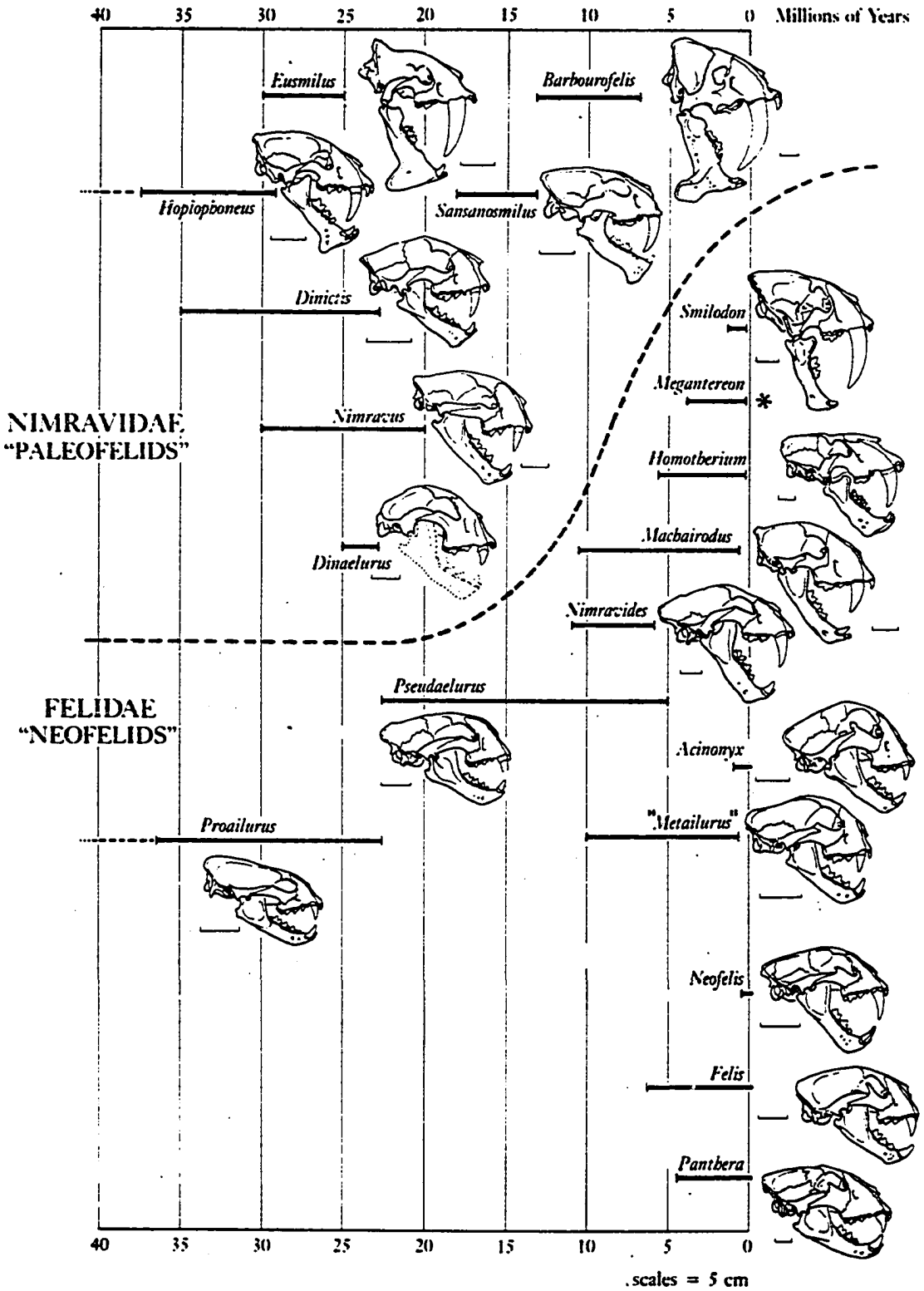
postglenoid foramen:	F	Y	V	H	C	U	O	R	M	P
reduced	+	+	+	+	-	-	+	-	-	?
absent	+	+	-	-	-	-	+	-	-	?

	F	Y	V	H	C	U	O	R	M	P
alisphenoid canal present	-	-	x	x	+	x	+	x	-	-

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Figure 1: The temporal ranges of sabertoothed and non-sabertoothed felids and nimravids. The scale on each skull and jaw represents 5 centimeters. "Metailurus" is in quotes because the species figured is "Metailurus" minor, a very different form from the type of the genus, M. major. My revision of the genus and description of a related form from North America, currently in preparation, will reassign "M." minor to the North American genus Pratifelis, and demonstrate the affinities of Pratifelis to Acinonyx, and the affinity of Metailurus major to the pantherines. Megantereon not figured. Modified from Neff (1982), and partly after Tedford (1978).

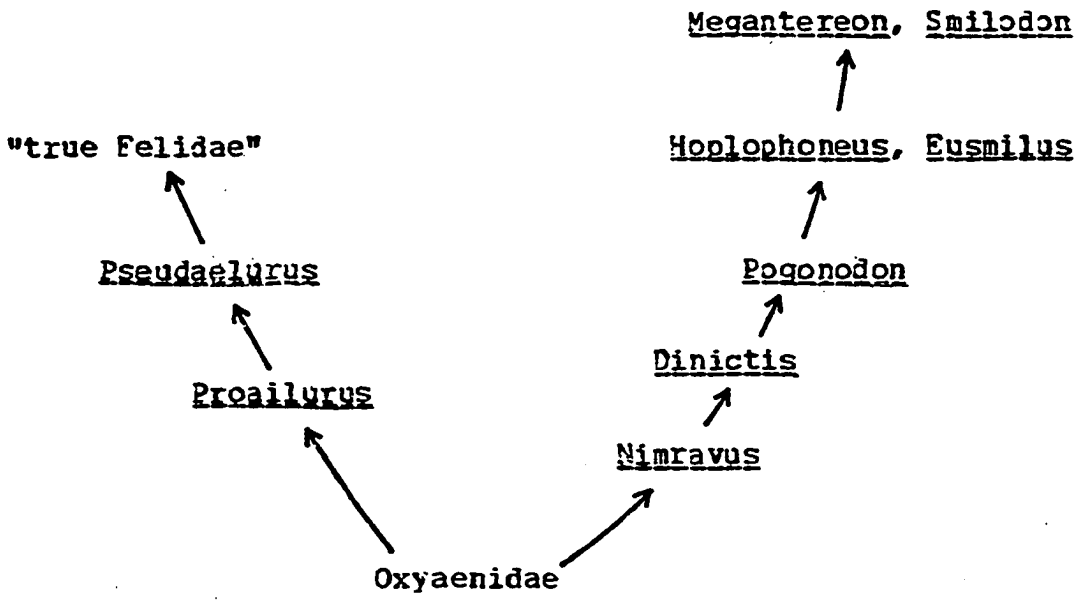
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Figure 2: The phylogeny described in the text of Cope (1880a) contrasted with the classification proposed therein. The first subgroup in the Nimravidae was only tentatively assigned to that family. The names in quotes were the ones used by Cope, and have been replaced here by their current designations. The features upon which each family was based are listed below the classification. (P) denotes primitive character states, (D) derived character states, and (E) erroneous description or interpretation of the anatomy, according to the present analysis.

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FELIDAE

I Megantereon ("Drepanodon")
Smilodon

II Acinonyx ("Cynaelurus")
Panthera ("Uncia")
Uncia
Neofelis
Felis (including "Catolynx")
Lynx

NIMRAVIDAE

(I Proailurus
Pseudaelurus)

II Nimravus

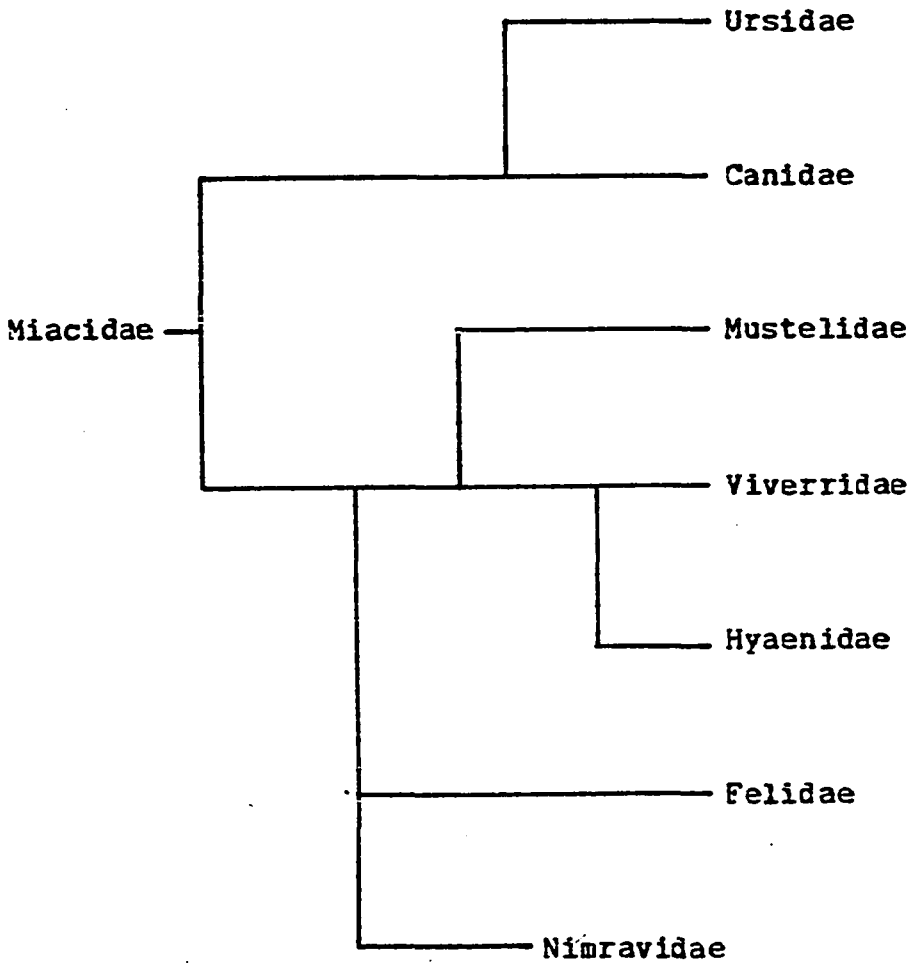
III Dinictis
Pogonodon
Hoplophoneus
Eusmilus

Character	Condition in: FELIDAE	NIMRAVIDAE
alisphenoid canal	absent (D)	present (P)
postglenoid foramen	absent (D)	present (P)
posterior carotid foramen & posterior lacerate foramen	confluent (D)	distinct (E)
hypoglossal foramen and posterior lacerate foramen	confluent (D)	distinct (P)

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Figure 3: The phylogenetic relationships among the families of Carnivora suggested by W. B. Scott. The Procyonidae were omitted by Scott because of lack of information. (From Scott (1889); spacing and geometry of the lines are his, including the offset position of the Nimravidae.)

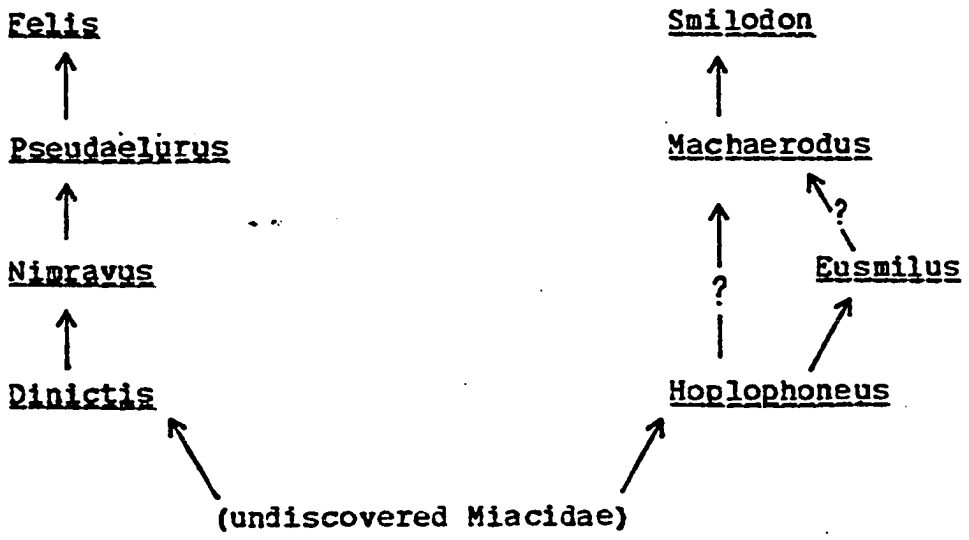
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Figure 4: The phylogeny described in the text of Matthew (1910) and the corresponding classification. Many characters are discussed in the text of his paper; however, the anatomical basis for his classification may be justly summarized as sabertooth versus non-sabertooth morphology.

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F E L I D A E

Felinae

Felis
Pseudaelurus
Nimravus
Dinictis

non-sabertooth morphology (P)

Machaerodontinae

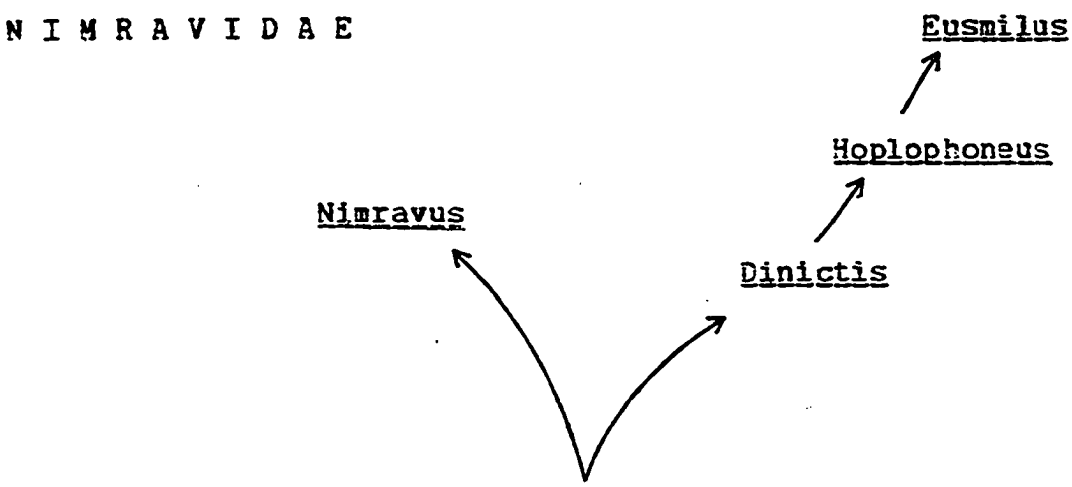
Smilodon
Machaerodus
Eusmilus
Hoplophoneus

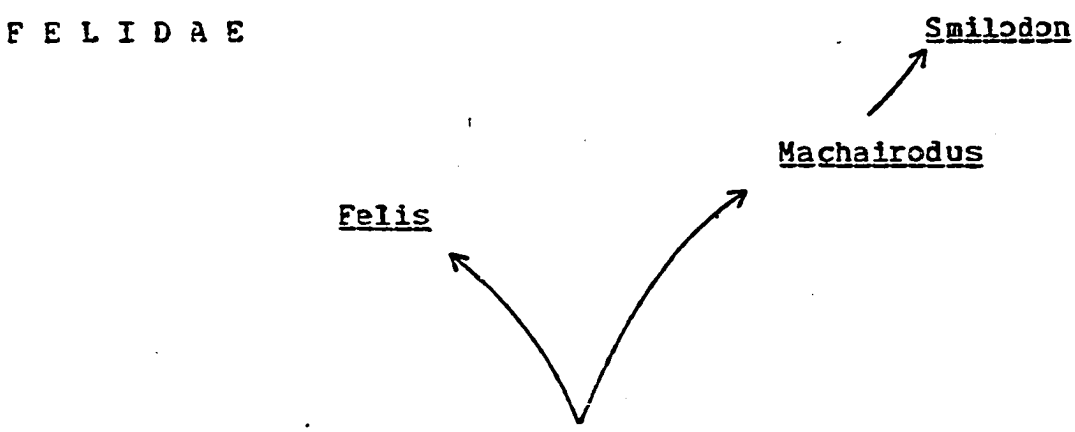
sabertooth morphology (D)

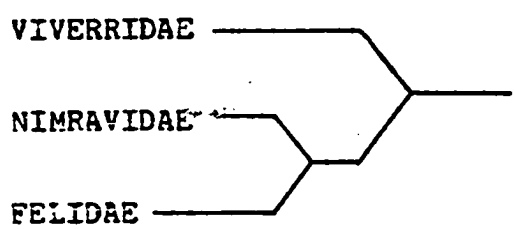
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Figure 5: Hypotheses for parallel phylogenies of the Nimravidae and Felidae, put forth in the text of Piveteau (1931). Both groups have a small-canined representative (left) and a sabertoothed lineage (right). Further discussion in his text concludes that these two families are sister groups and together are most closely related to the Viverridae; these relationships are summarized by the bottom diagram.

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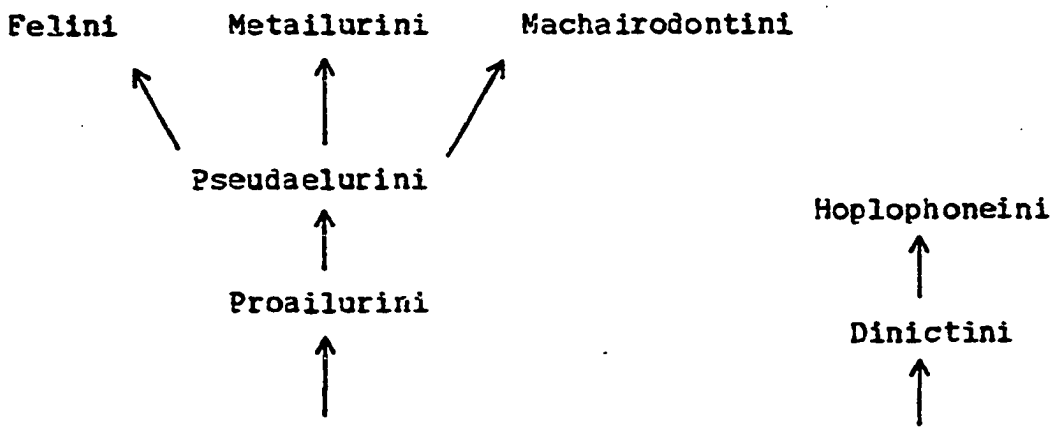




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Figure 6: The phylogenetic relationships among the tribes in the family Felidae, described in the text of de Beaumont (1964).

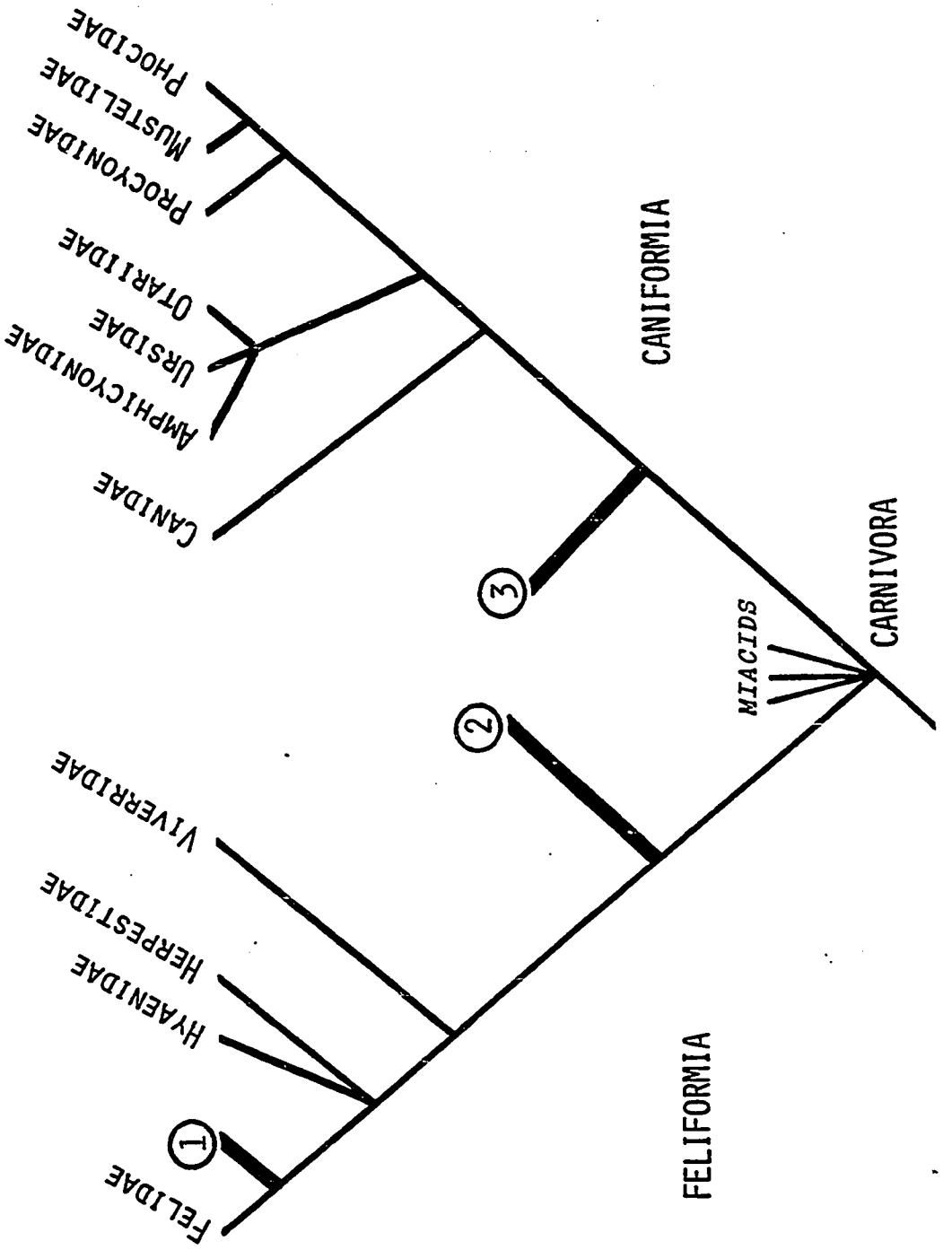
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Figure 7: A cladogram depicting my current working hypothesis of the phylogenetic relationships among the families of the order Carnivora. The positions marked "1", "2", and "3" represent the three different hypotheses of relationship of the family Nimravidae to the other Carnivora proposed to date. Position "1" includes those schemes in which mixed lineages were proposed, such as Matthew (1910); in such arrangements, monophyletic groups corresponding to the Felidae and Nimravidae were not recognized. Arrangements that recognized distinct families but considered them to be sister groups, such as those of Piveteau (1931) and Martin (1980), are also included in "1". Tedford (1978) and Baskin (1981) recognized that other feliform families were more closely related to the Felidae than were the Nimravidae--position "2". Finally, Flynn and Galiano (1982) postulated a caniform relationship (position "3").

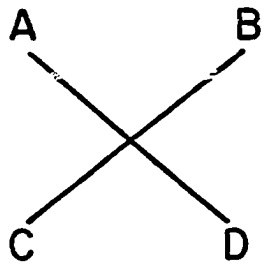
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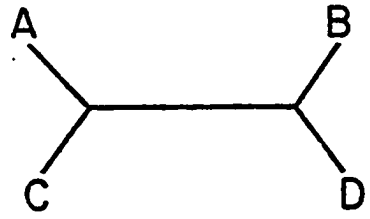


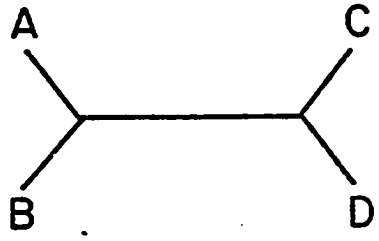
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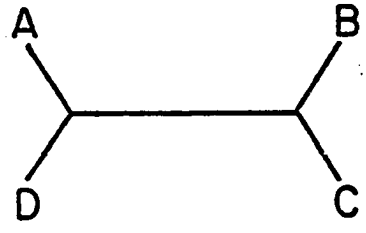
Figure 8: The four networks possible for four taxa.

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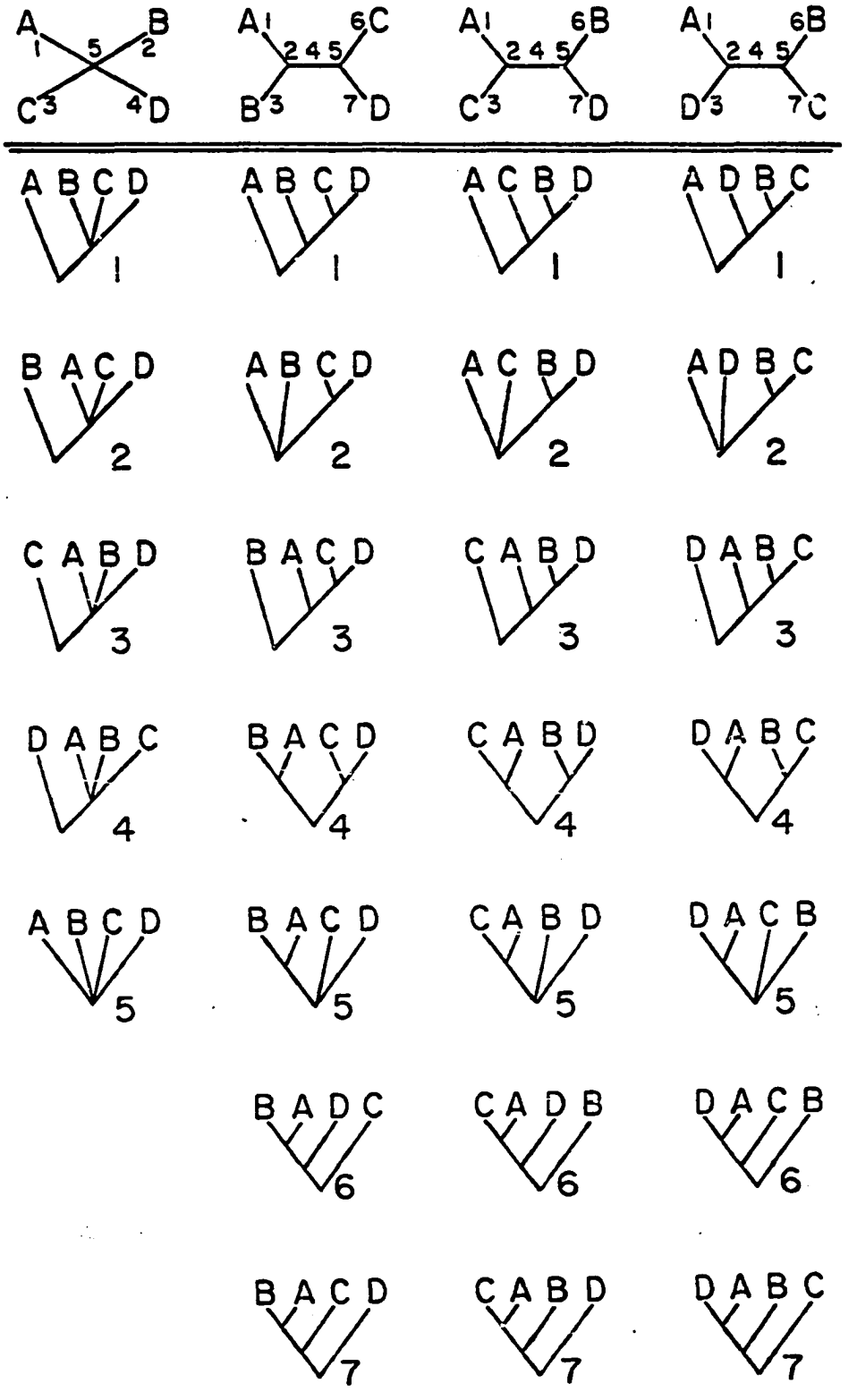




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Figure 9: The set of trees for each of the four possible networks for four taxa. The position of the root for each tree on its network is marked by the tree's number.

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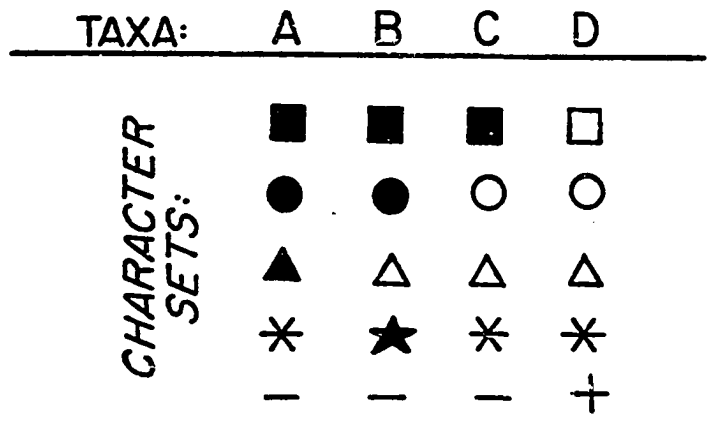


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Figure 10: A hypothetical data matrix and best-fit network for four taxa, A, B, C, and D. A) Hypotheses of homology have been constructed producing five sets of homologues (five "characters"), each comprising two states. No hypotheses of polarity have been made; for each character or set of homologues, it is not yet decided which feature is the non-informative primitive character state and which the character with restricted distribution, the informative derived character state. B) A distance matrix helps derive and check the network. Each number is the number of characters for which the two taxa differ. For example, B and D have different states for four characters, B and C for two. C) The network minimally explaining the character differences. The hypotheses of homology are placed next to the appropriate branches, with double-headed arrows indicating the lack of a hypothesis of polarity. The number of character changes are shown below each line for comparison with the distance matrix: for example, B is separated from D by three links of lengths 1, 1, and 2, which total to 4, and B from C by 1, 1, and 0--a total of 2.

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A.

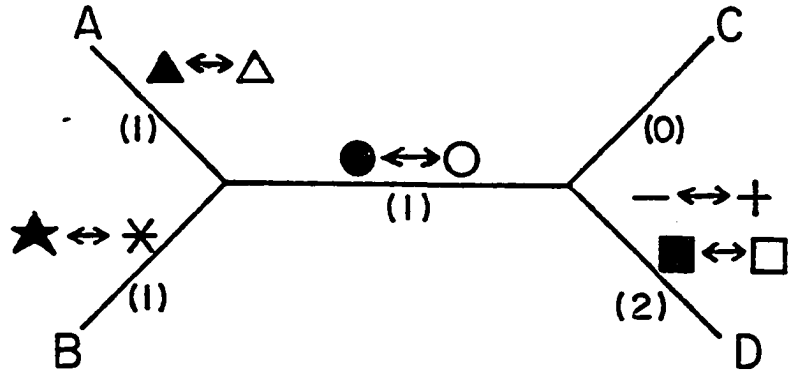


B.

	A	B	C	D
A	0			
B	2	0		
C	2	2	0	
D	4	4	2	0

DISTANCE MATRIX

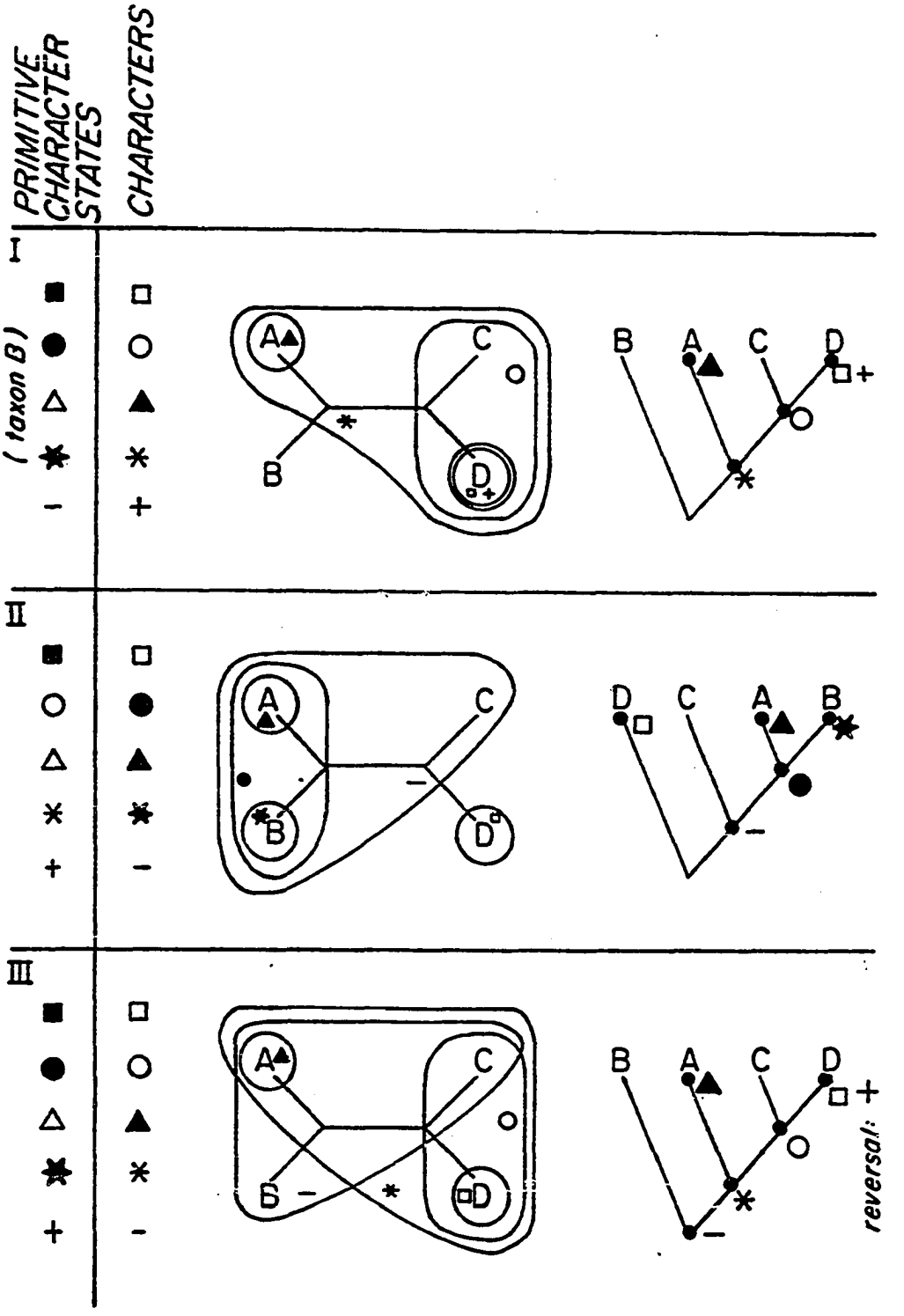
C.



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Figure 11: Three examples of sets of polarity hypotheses and the resulting cladograms, for the data set in Figure 10. The first column lists the uninformative primitive character states, and the second column the characters hypothesized to give us information about relationship. The diagram in the third column highlights the distribution of each informative character on the network; this same information is summarized in the cladogram in the fourth column. Example I: Taxon B has been designated the out-group to (ACD); character states that do not occur in B are thought derived for (ACD) or some subset therein. Example II: A character-by-character analysis of polarity may easily result in a set of primitive states that are not found in any sample taxon. In this case, one character's distribution is restricted to (D), the taxon in the "out-group position" relative to (ABC). Example III: A character-by-character analysis of polarity may also result in a set of characters whose distributions conflict, as shown by the lack of complete nesting of the character distributions on the network. In this case, if the polarities are accepted, the simplest hypothesis is that taxon D exhibits a reversal.

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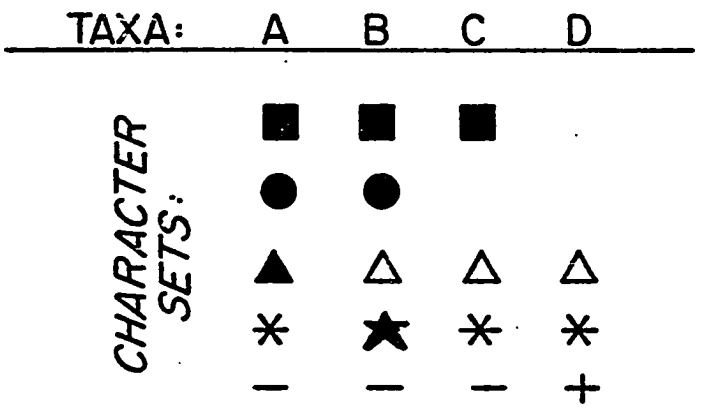


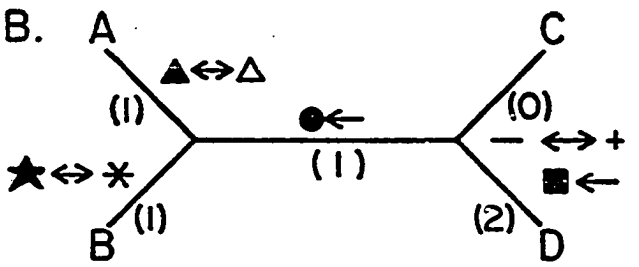
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Figure 12: The data set, network, and cladogram for a data set with two novel characters. The "character state" for character 1 in taxon D and character 2 in taxa C and D was the absence of any feature recognizably homologous to the character in taxa A, B, C, and A and B respectively. Absence (rather than loss) of a feature cannot be a character. Therefore, outgroup comparison is not required to recognize the informativeness of novel characters. A) The data set with no character states shown in those cases in which any homologous feature is lacking. B) The network minimally explaining the character differences. The two novel characters are shown with a single-headed arrow since the a priori assumption is that such characters of a limited distribution are evolutionary novelties unless character conflicts show otherwise. (see text) C) The sets implied by the novel characters, and D) the cladogram representation.

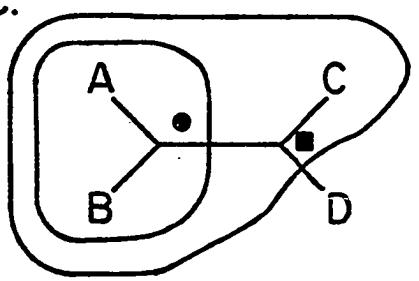
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A.

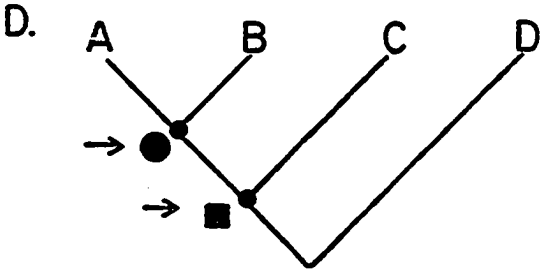




C.



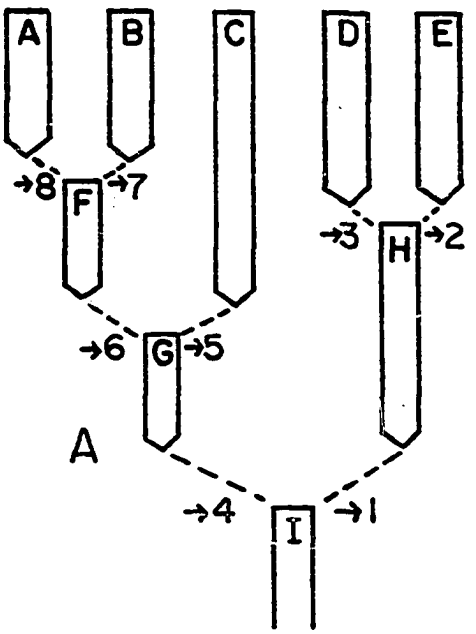
D.



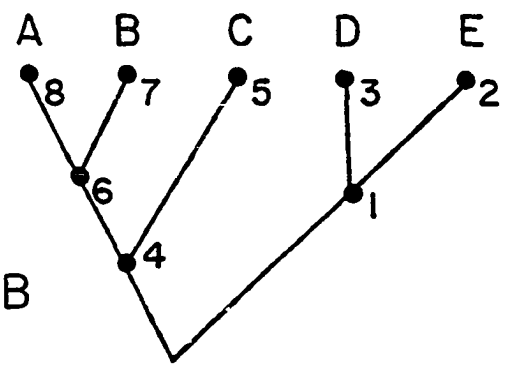
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Figure 13: A hypothetical phylogeny and the corresponding cladograms. A) A dichotomous phylogeny in which character transformation occurred in each daughter species at the time of speciation and the ancestral species became extinct. B) The dichotomous cladogram that would be produced if all relevant characters were found and interpreted correctly, and no ancestral taxa were sampled. C) The multichotomous cladogram that would result from the phylogeny in A if all taxa were sampled and no mistakes about character distributions were made.

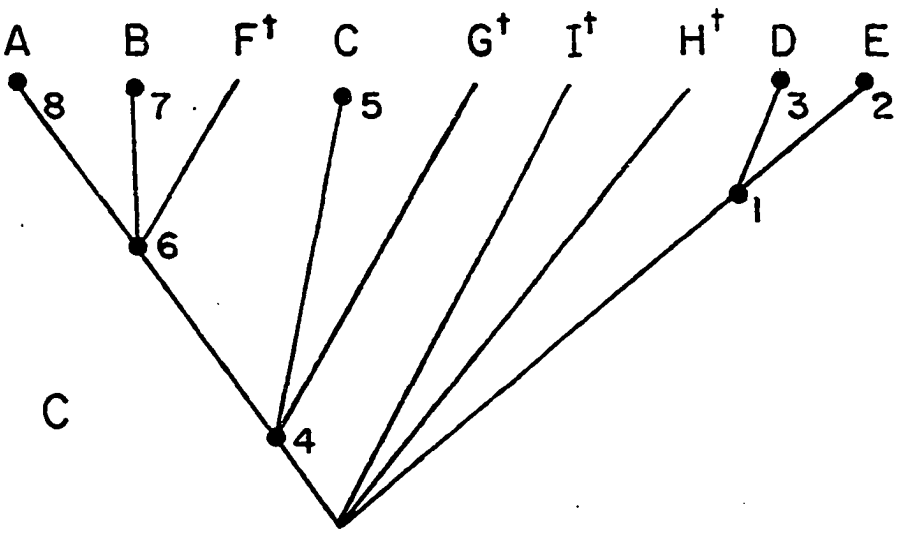
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A



B



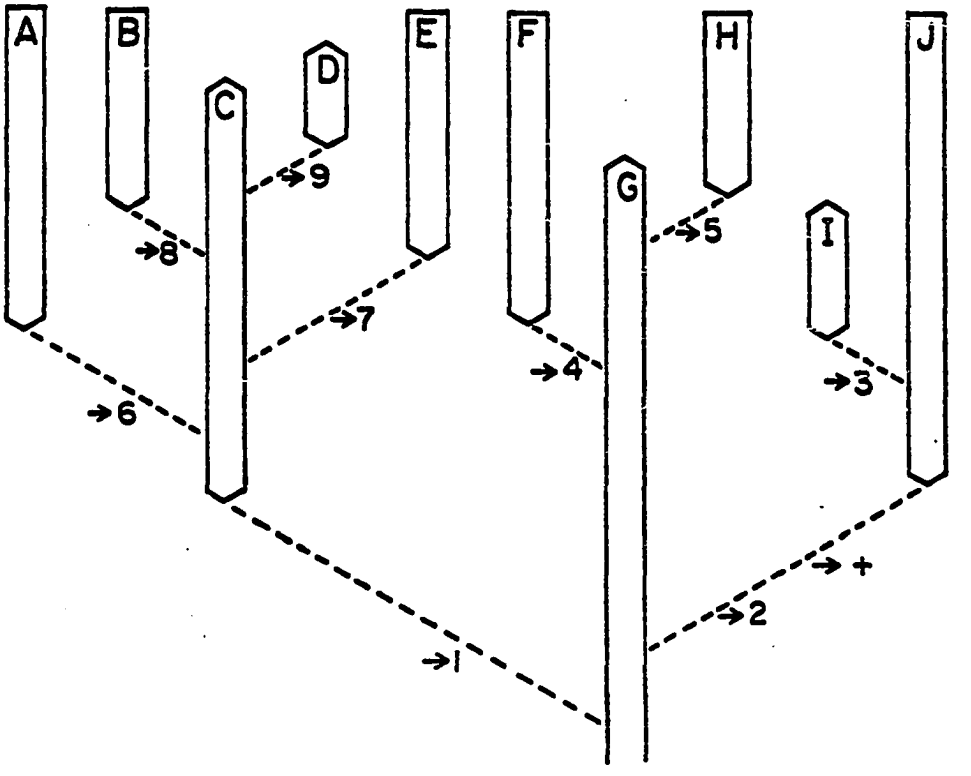
C

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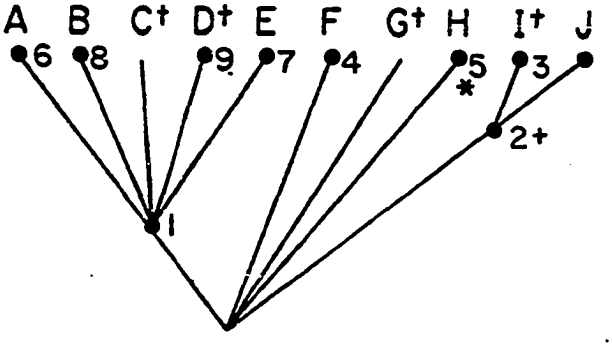
Figure 14: A) A hypothetical phylogeny in which character transformation occurs only in the diverging lines (small founder populations, for example), and ancestral taxa persist without change contemporaneously with descendant taxa. B) The cladogram for the phylogeny in A, if all taxa were sampled, all relevant characters were recognized, and no mistakes about homology were made. C) An incorrect but further resolved cladogram resulting from an incorrect hypothesis of homology. Under the current cladistic methodology, this error could never be discovered and corrected.

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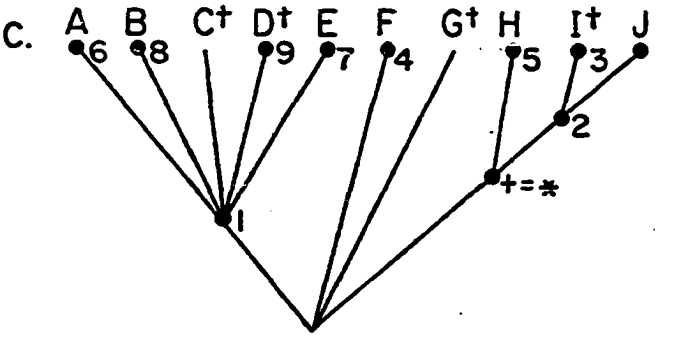
A.



B.



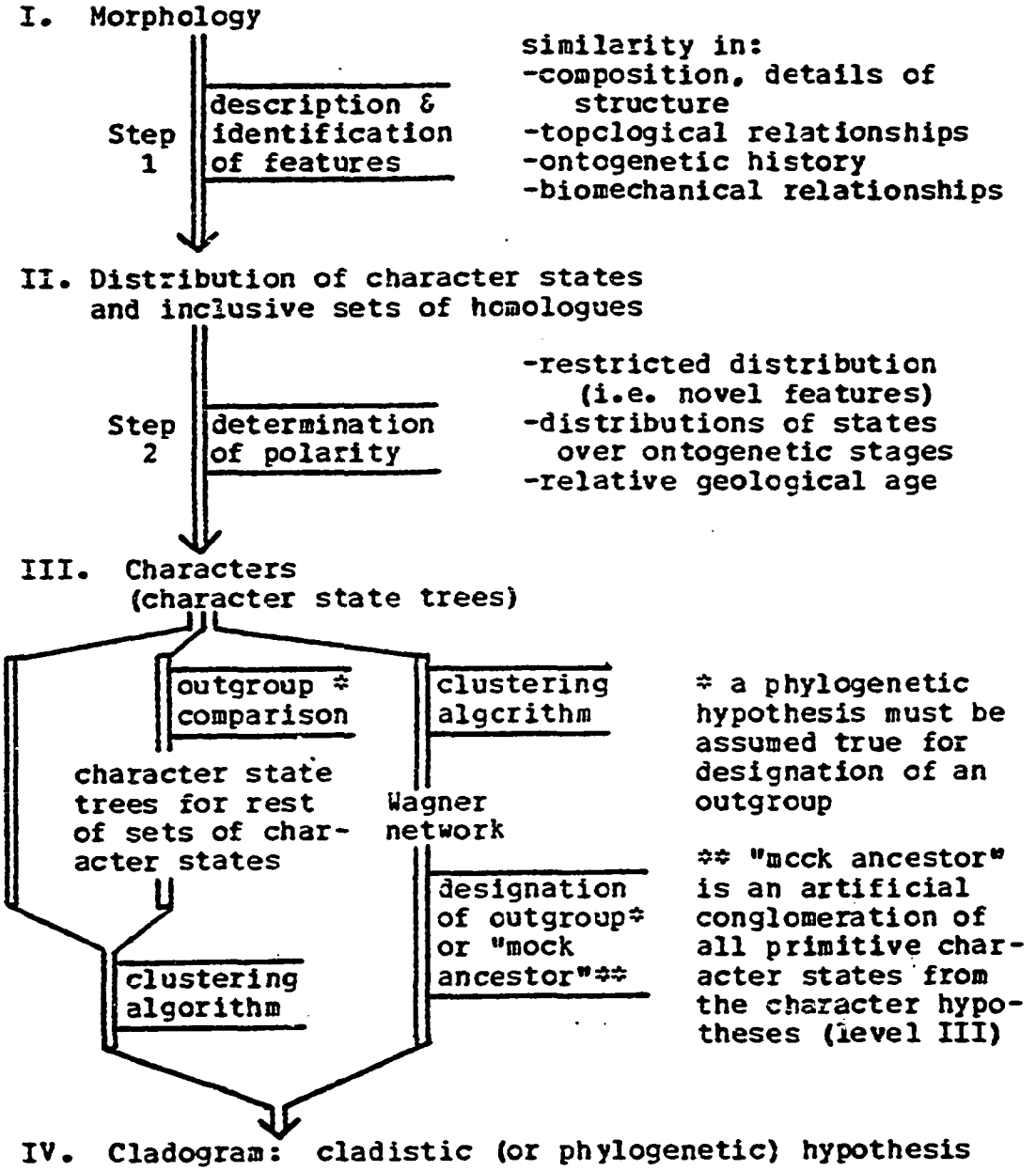
C.



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Figure 15: An outline of the steps and levels in CHARACTER ANALYSIS and CLADISTIC ANALYSIS, and lists of criteria that provided evidence for hypotheses at each step. Although "clustering algorithm" is indicated for a step in Cladistic Analysis, it should be kept in mind that a variety of algorithms have been proposed, and that none guarantee the shortest network or tree without exhaustive search (i.e., the Steiner tree problem is not yet solved).

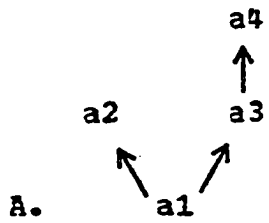
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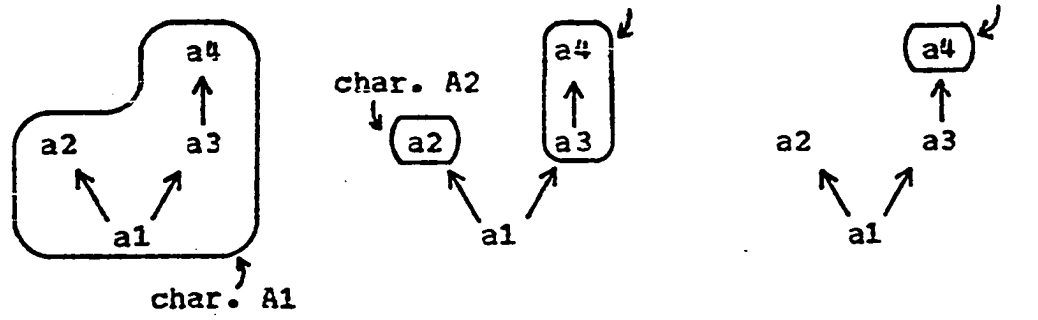
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Figure 16: A diagram showing the relationship between character states and characters. Characters are monophyletic sets of character states. A primitive character state is not itself a character (e.g., a3 relative to a4), but is part of a character. A) The hypothesized character state tree. B) The monophyletic sets of character states constituting the characters. C) The nesting relationship of the four characters.

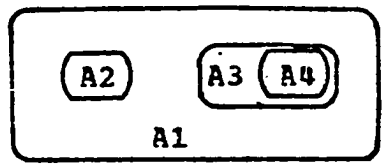
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A.



B.



C.

example:

a1 = pectoral fins

a2 = pectoral fins with large spines (catfishes)

a3 = tetrapod forelimb

a4 = bird wing

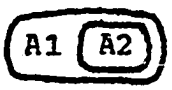
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Figure 17: Two examples illustrating the use of ontogenetic stages as additional elements with which to assess the generality of the distributions of character states. See text for discussion.

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A.

taxa:	X	Y
character state in adult:	a1	a2
ontogenetic sequence:	a1 ↑ a1	a2 ↑ a1



character state tree:



example:

a1 = horizontal, horseshoe-shaped ectotympanic

a2 = expanded, vertical ectotympanic

B.

taxa:	X	Y
ontogenetic sequence:	a0 ↑ a2 ↑ a1	a0 ↑ a2 ↑ a3

example:

a0 = no (embryonic) membranes present (adult condition)

a1 = simple chorion derived from ectoderm sheet

a2 = chorion associated with allantoic membrane

a3 = trophoblast

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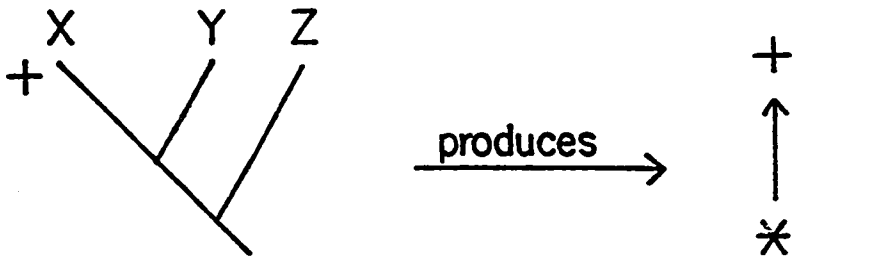
Figure 18: (A) A set of character states for which no polarity has been determined from character analysis. (B) The most parsimonious polarity assignment for each of the three possible cladograms, based on the cladistic hypothesis.

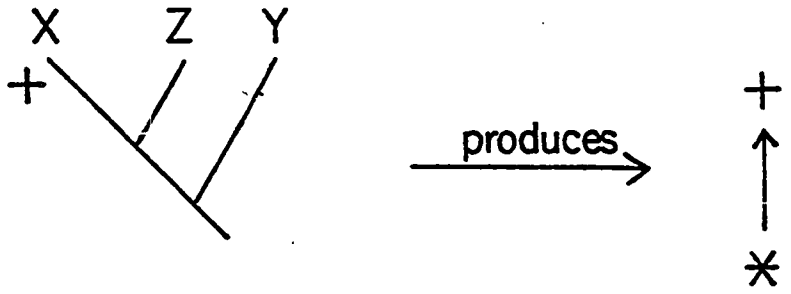
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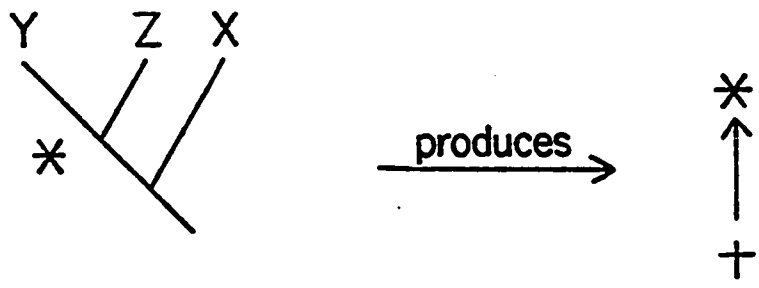
TAXON:	X	Y	Z
CHARACTER STATE:	+	*	*

CLADOGRAM

CHARACTER STATE TREE







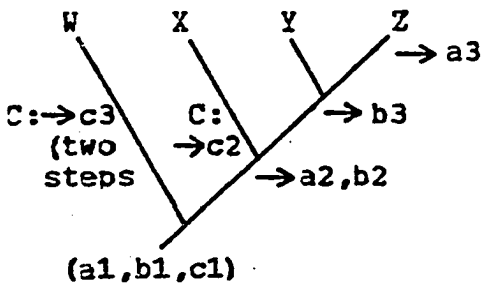
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Figure 19: An example comparing the results of maximizing parsimony at the cladistic level alone with the results if the evidence from character analysis is also considered. (B) In this example, reversing the polarity of one of the original transformation series in (A) results in an apparently shorter tree. (C) A comparison of the evolutionary histories of the features in set c, before and after the re-interpretation at the cladistic level. (D) The details of evolutionary histories from (C) if the original evidence from character analysis remains unrefuted, illustrating the decrease in overall parsimony resulting from contradicting the original character hypothesis merely to maximize local parsimony in the cladistic hypothesis.

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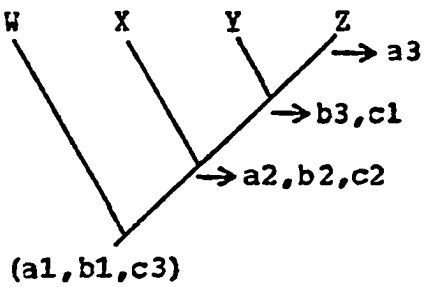
A.

taxa:	W	X	Y	Z	trees indicated by individual character analysis	individually predicted relationships
set a:	a1	a2	a2	a3	a1→a2→a3	W(XY(Z))
set b:	b1	b2	b3	b3	b1→b2→b3	W(X(YZ))
set c:	c3	c2	c1	c1	c1→c2→c3	(WX)YZ



B. 7 steps

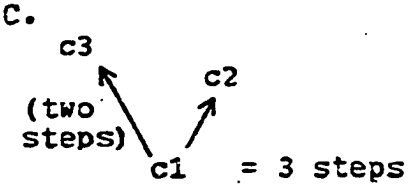
character states shown on cladogram congruent with majority of character hypotheses. Convergence required between W and X.



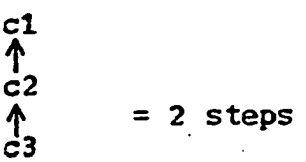
(6 steps)

character states shown on the same cladogram with the polarity of the incongruent character state tree reversed, producing an apparently shorter phylogenetic tree. (see text)

C.

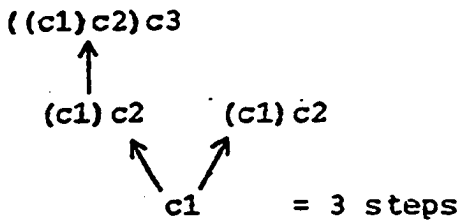


= 3 steps

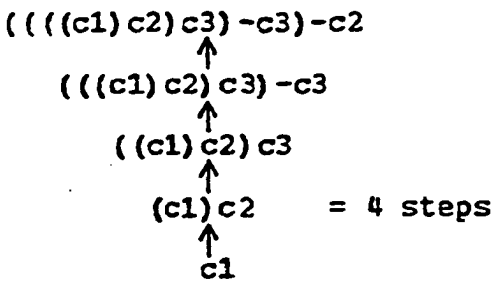


= 2 steps

D.



= 3 steps



= 4 steps

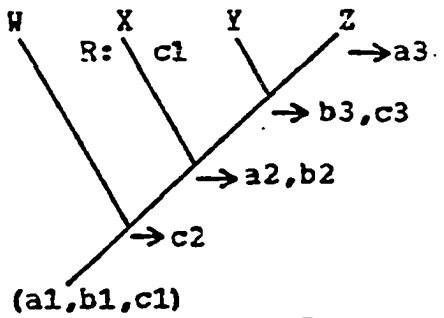
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Figure 20: A second example comparing the results of maximizing parsimony at the cladistic level alone with the results if the evidence from character analysis is also considered. (B) Re-ordering the states in one of the original transformation series in (A) (as in a Mickevich transformation series analysis) results in an apparently shorter tree. (C) A comparison of the evolutionary histories of the features in set c_2 before and after the re-interpretation at the cladistic level. (D) The details of evolutionary histories from (C) if the original evidence from character analysis remains unrefuted, illustrating the decrease in overall parsimony resulting from the abandonment of the original character hypothesis.

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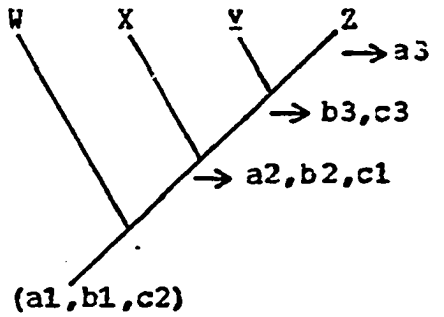
A.

taxa:	W	X	Y	Z	trees indicated by individual character analysis	individually predicted relationships
set a:	a1	a2	a2	a3	a1→a2→a3	W(XY(Z))
set b:	b1	b2	b3	b3	b1→b2→b3	W(X(YZ))
set c:	c2	c1	c3	c3	c1→c2→c3	X(W(YZ))



B. 7 steps

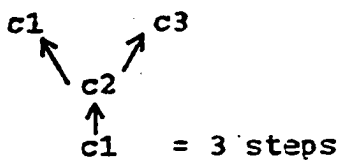
either c2 is developed convergently in W and (YZ) or reverses to c1 in X; in either case, an 'extra' step is required.

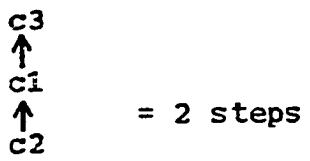


(6 steps)

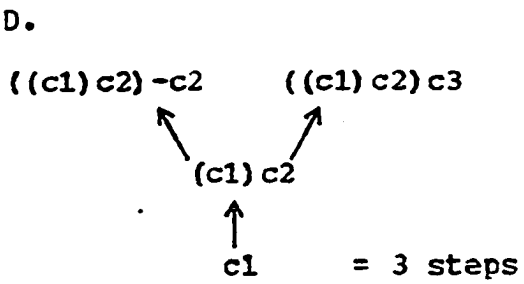
ordering of character states in transition series c is changed to c2→c1→c3, which results in an apparently shorter tree.

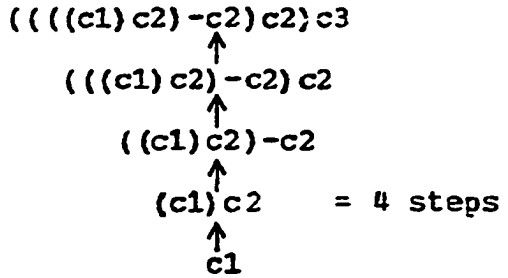
C.





D.





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Figure 21: A diagram summarizing the restriction of the number of possible character state trees under a restrictive transformationist assumption. (A) If a2 is assumed to be intermediate, the only trees possible are those congruent with the network with a2 between a1 and a3. (B) Such an assumption precludes consideration of the six other trees corresponding to the two other possible networks.

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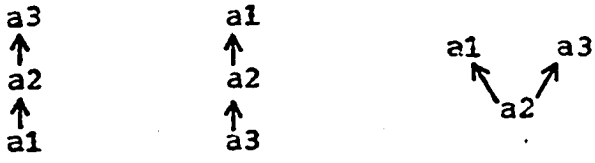
A.

a1 = small mastoid process
a2 = moderately sized, slightly elongate mastoid process
a3 = large, elongate mastoid process

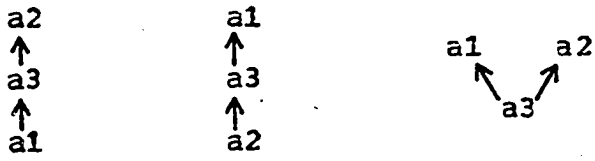
network of character states if a2 is assumed intermediate:

a1—a2—a3

3 possible character state trees under this assumption:

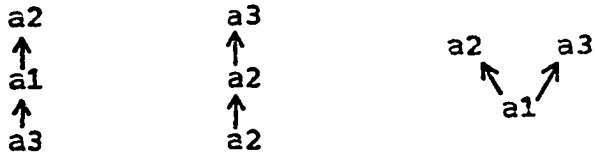


B. 'inherently illogical trees':



network:

a1—a3—a2



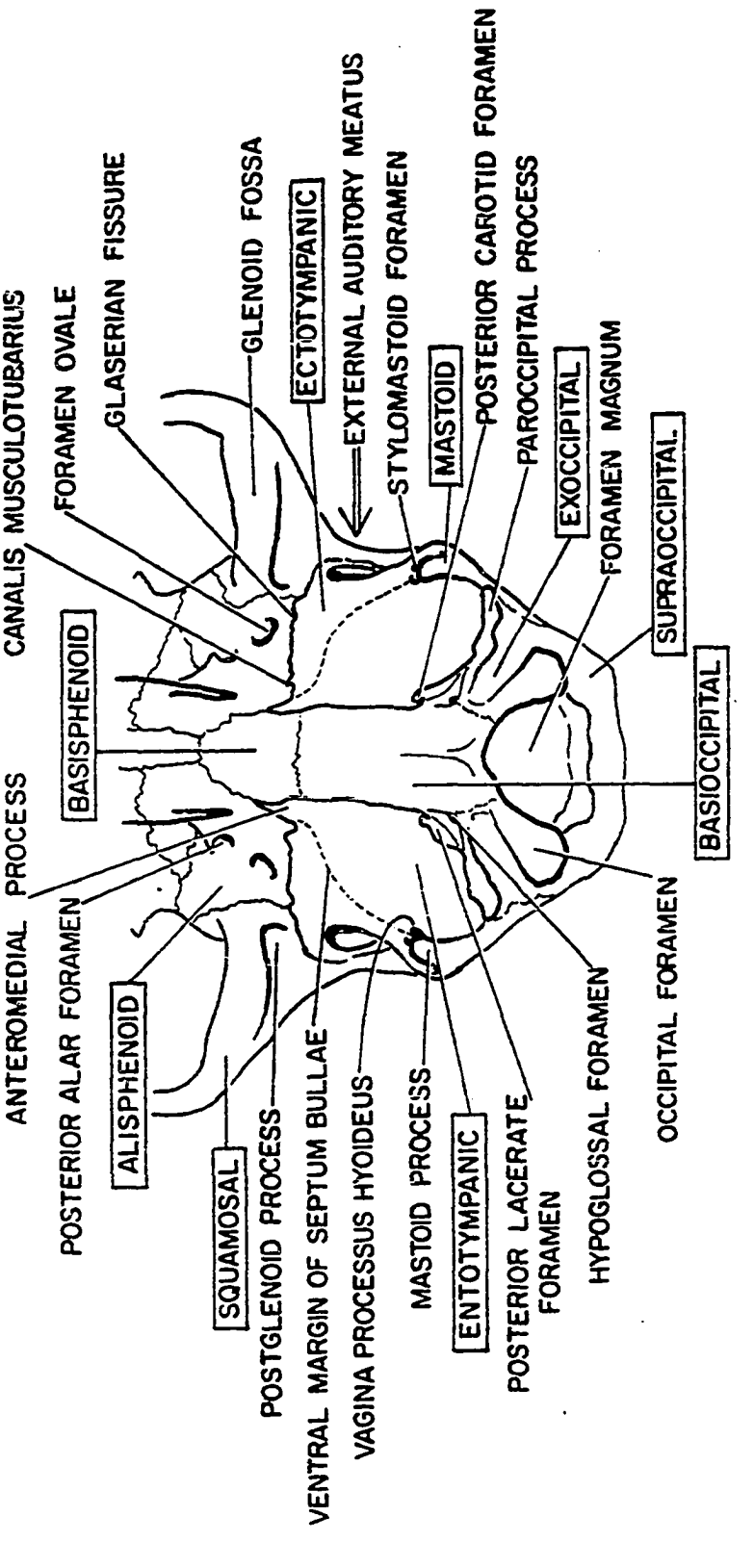
network:

a2—a1—a3

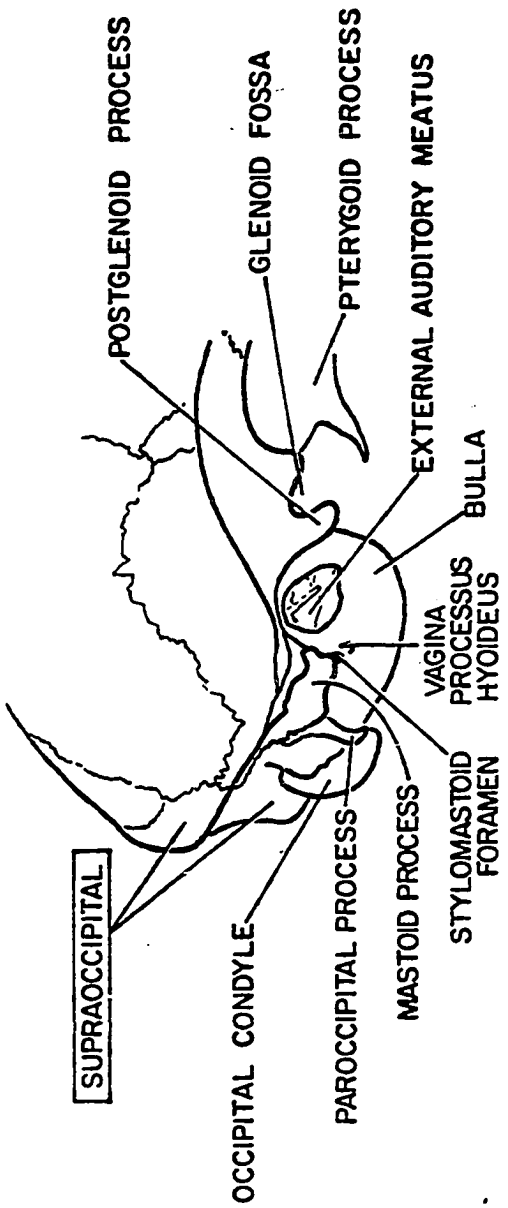
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Figure 22: The bones, structures, foramina, and other features frequently mentioned in the text are shown on diagrams of Felis catus. A) The basicranial region, ventral view. B) Right lateral view. C) Intracranial anatomy of the right otic region of the skull. Boxes denote the names of bones per se; other terms refer to structures which may be composed of one or more of these bones.

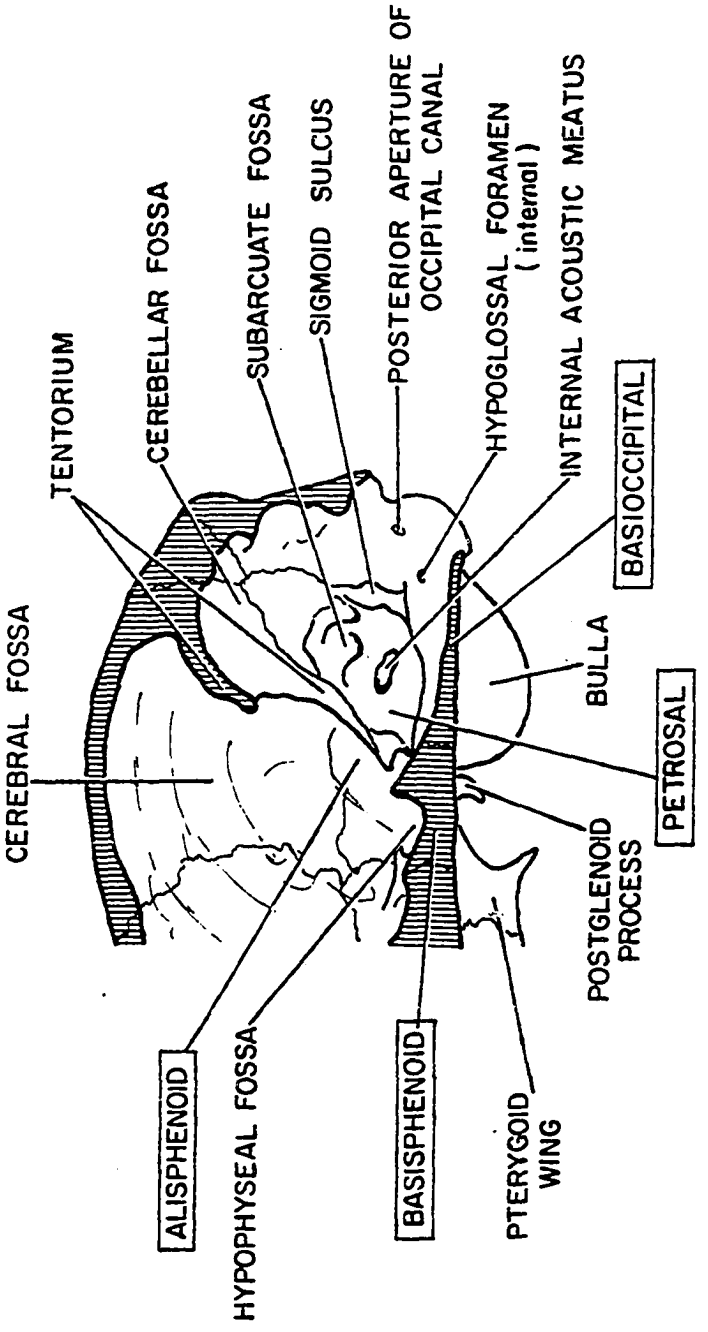
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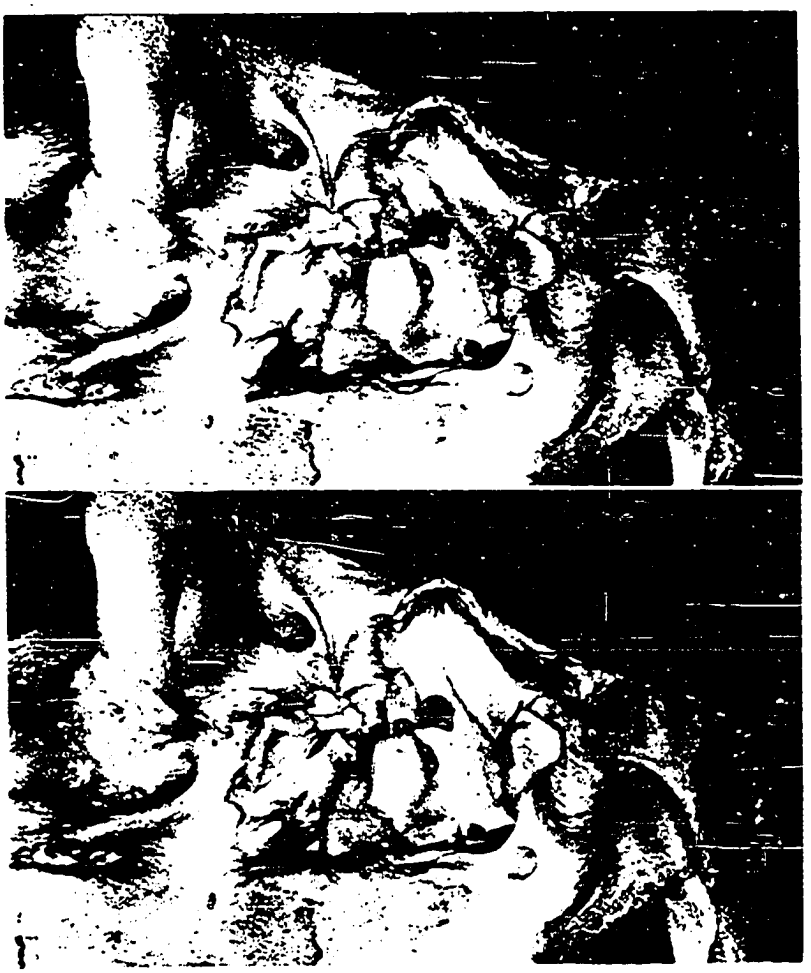
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Figure 23: Stereo pair illustrating the structures of the tympanic roof of the left auditory region in a carnivoran, Nasua nasua (AMDM CA:1286, subadult). Most of the bulla has been removed. (Corresponding line drawing with labels on page following photographs.)

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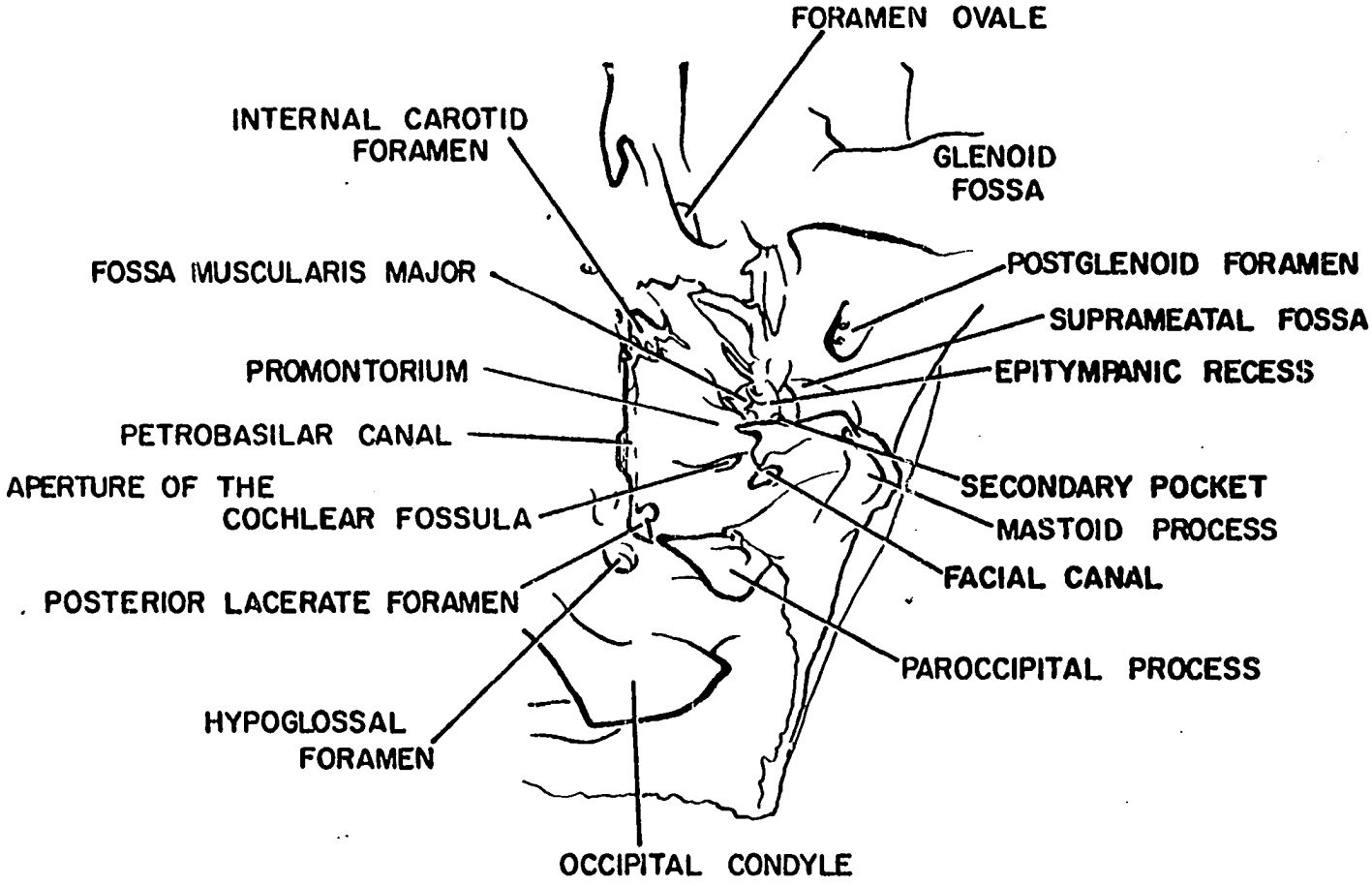
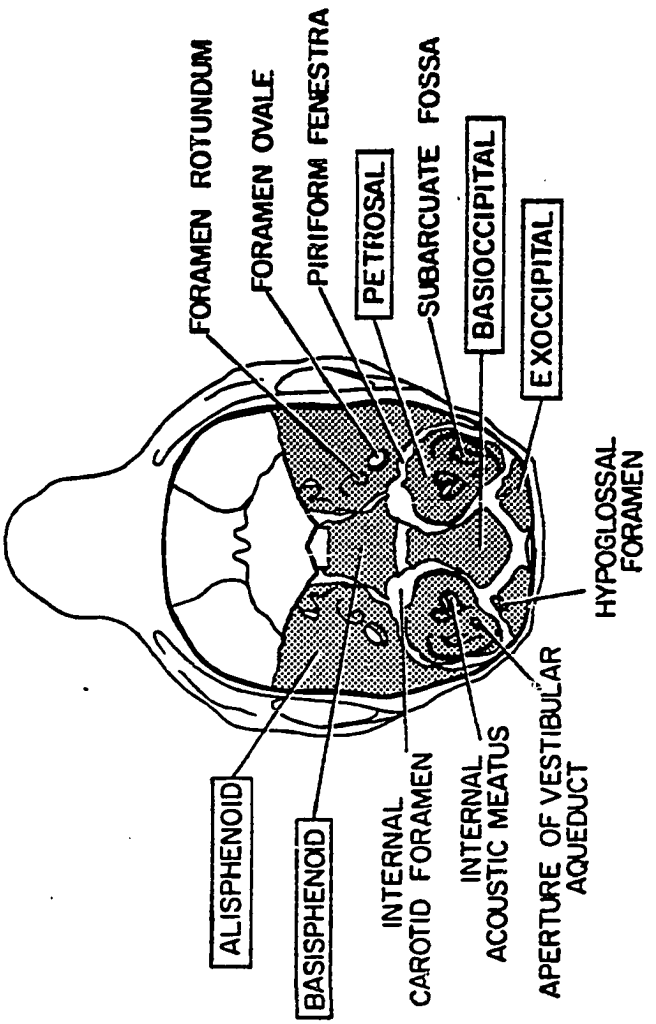
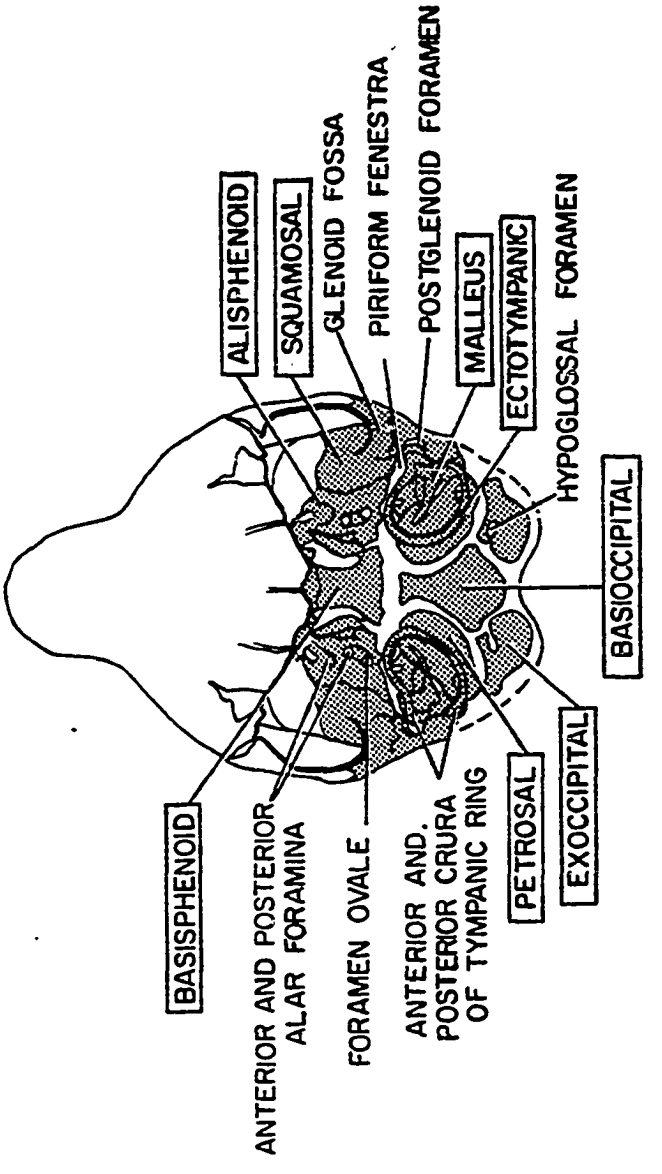


Figure 24: Diagram of the ossified elements in the basicranium of a juvenile Canis (four days old). A) Dorsal view. B) Ventral view. Boxes denote bones rather than specific structures. (Modified from Figure 243 in Starck, 1967: 481.)

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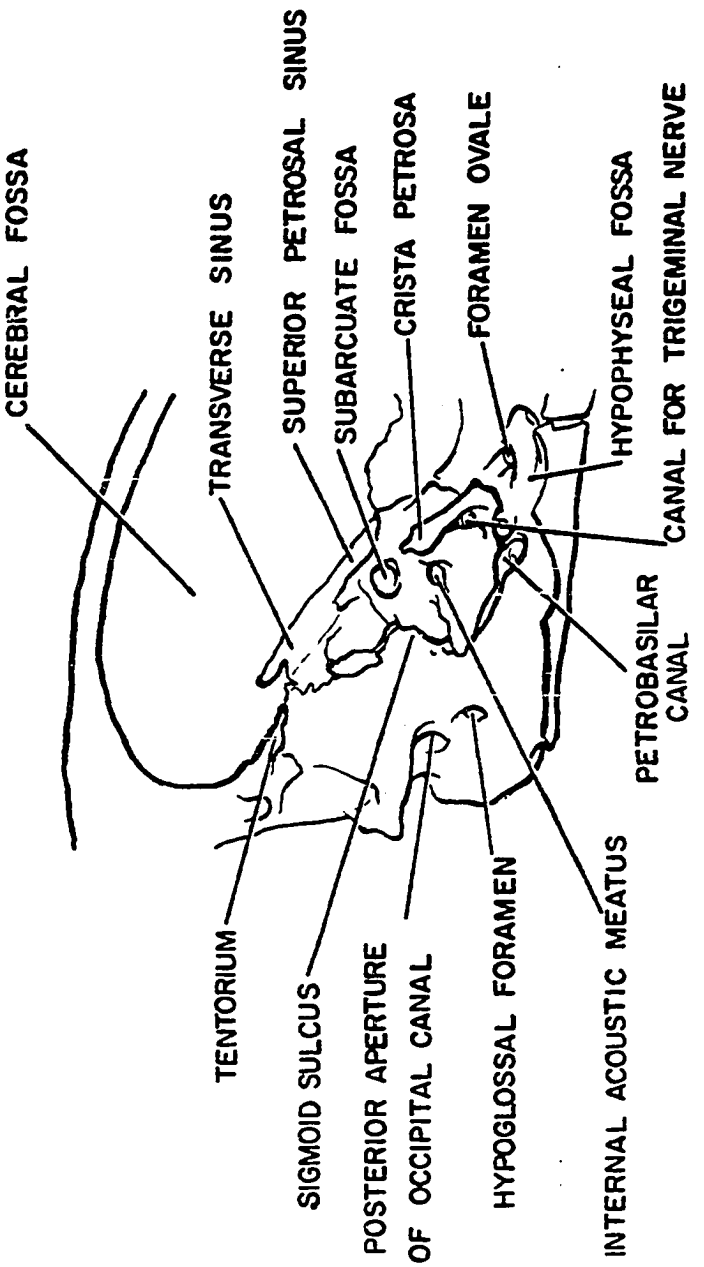
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Figure 25: Stereo pair of a hemisected skull of Canis latrans (AMNH AINS:668-B) illustrating the intracranial structures in the left otic region of an arctoid carnivoran. Labelled diagram on the next page following photographs.

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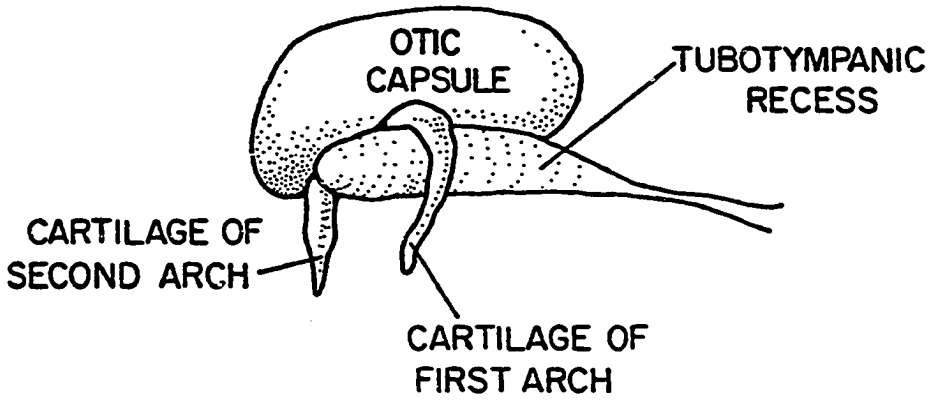
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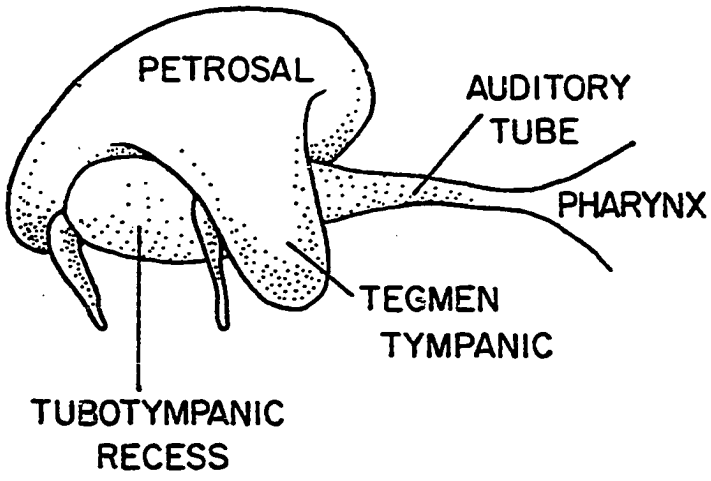


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Figure 26: Diagrammatic summary of the relationships between the otic capsule (to become the petrosal), the tubotympanic recess defined by the pouch from the pharynx, and the cartilages of the pharyngeal arches. (Taken from Gardiner et al., 1960.)

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Figure 27: Diagram of the middle and inner ear of a dog. Modified from Getty et al., 1956: 366.

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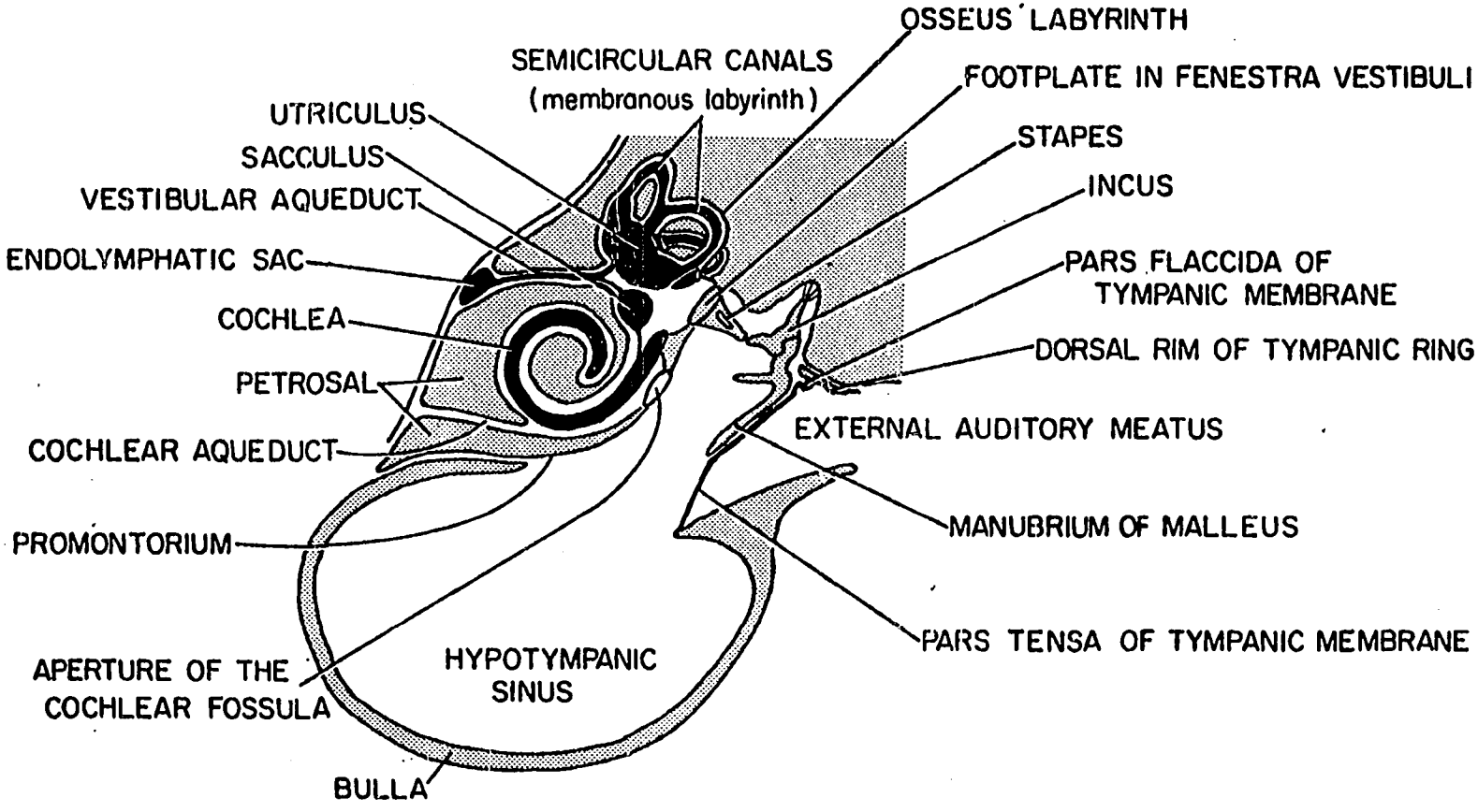
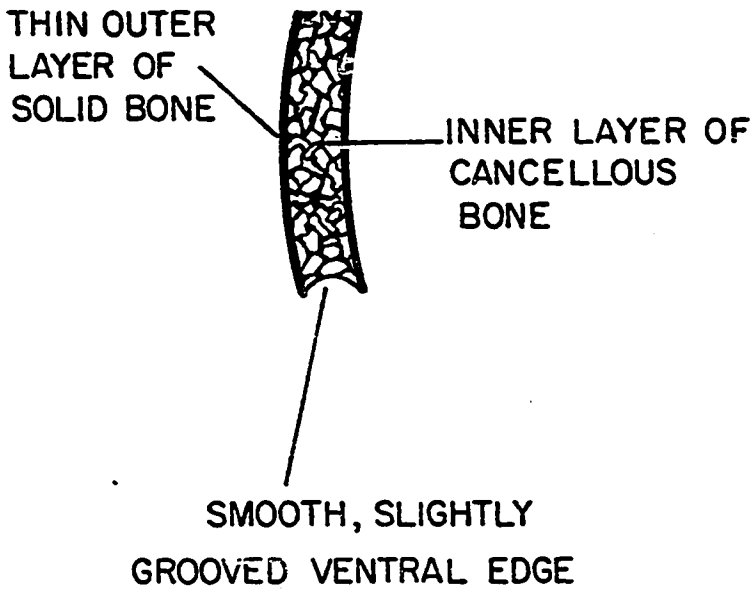


Figure 28: Diagrammatic cross section of the entotympanic in Dinictis, showing the sandwich-like construction of that element characteristic of all nimravids studied here except Barbourofelis.

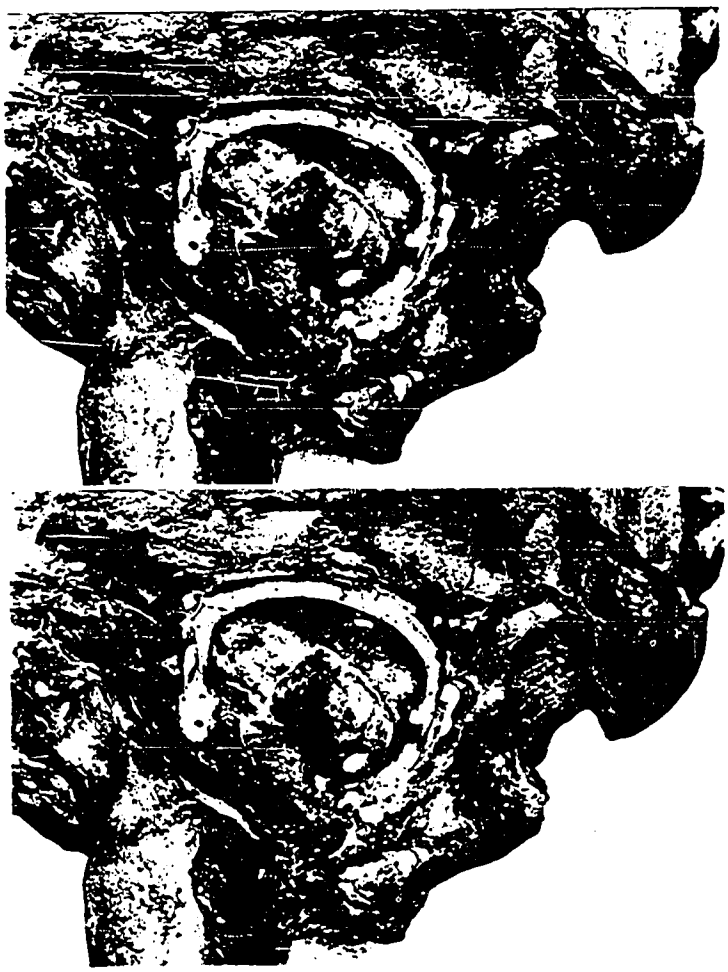
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Figure 29: Stereo pair of the right auditory region of AMNH 6937, the type of Dinictis cyclops Cope.

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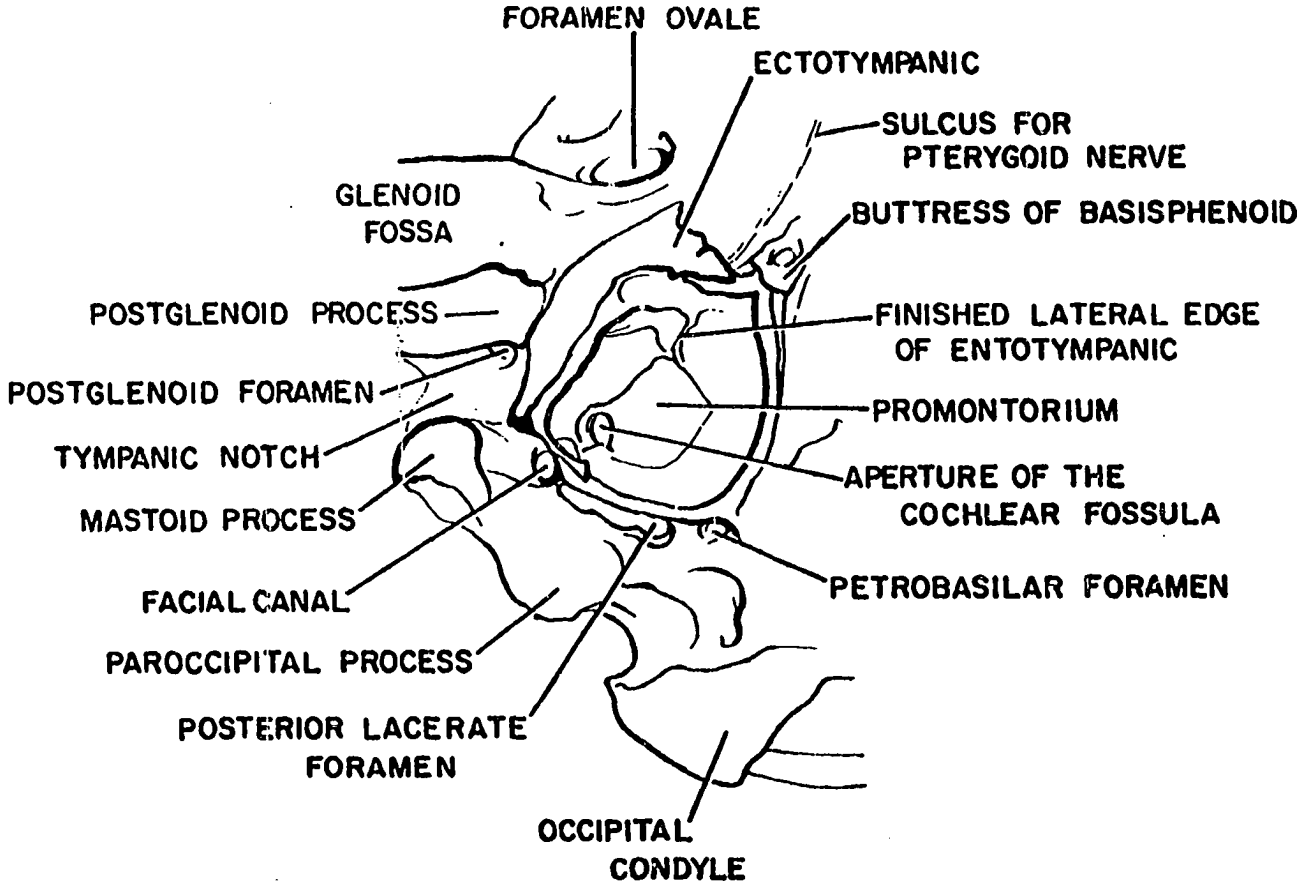
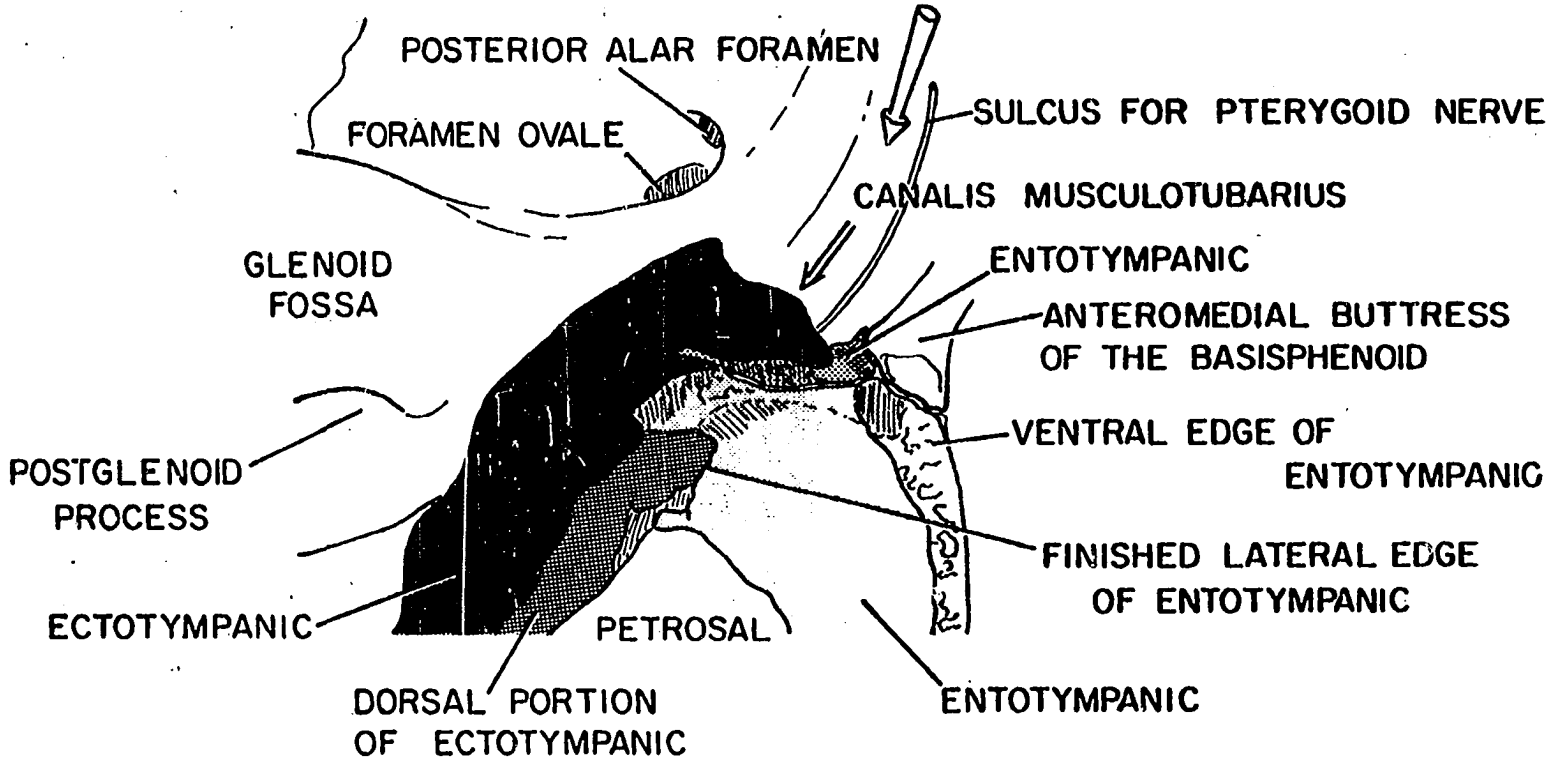


Figure 30: Diagrams illustrating the relationships between the parts of the bulla at its anterior end in Dinictis cyclops AMNH 6937. The large arrow in each drawing specifies the angle of view of the other drawing. The most darkly shaded element is the ventral part of the ectotympanic; the next darkest is the dorsal part of the ectotympanic ring, lying on the tympanic roof. The lightest stipple shades the main portion of the (caudal?) entotympanic, whereas the slightly darker stipple anteriorly shades the portion of the entotympanic that looks as if it might be a separate element. Lined portions of the ecto- and entotympanic denote areas of the bones inferred but currently hidden by matrix (and too fragile to clean further). If an channel in the basisphenoid for the anastomosis of the ascending pharyngeal artery with the internal carotid artery is present, it is dorsal to the entotympanic. The anterior aperture of that channel is just barely visible deep in the canalis musculotubarius, on the medial wall.

A) Ventral view of the anterior portion of right auditory region of AMNH 6937. B) Anteromedial and ventral view of same auditory region.

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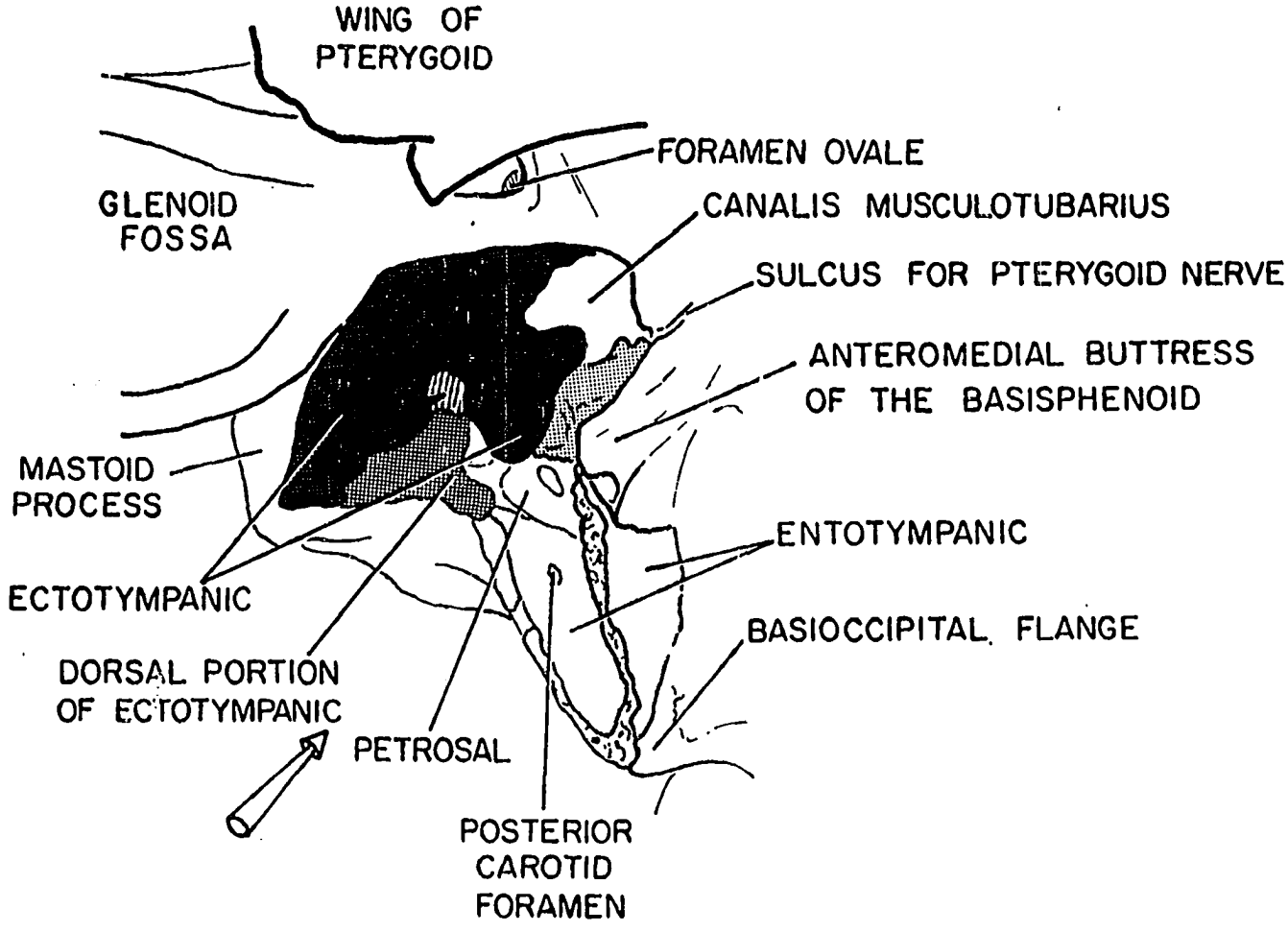
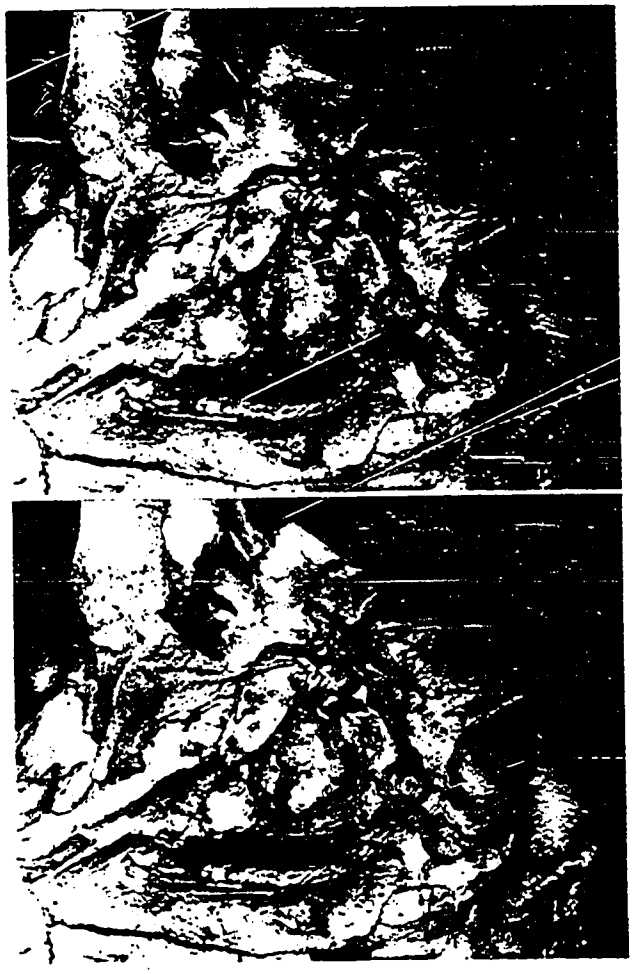


Figure 31: Stereo pair of the left auditory region of *Dinictis* sp., F:AM 62034, ventral view.

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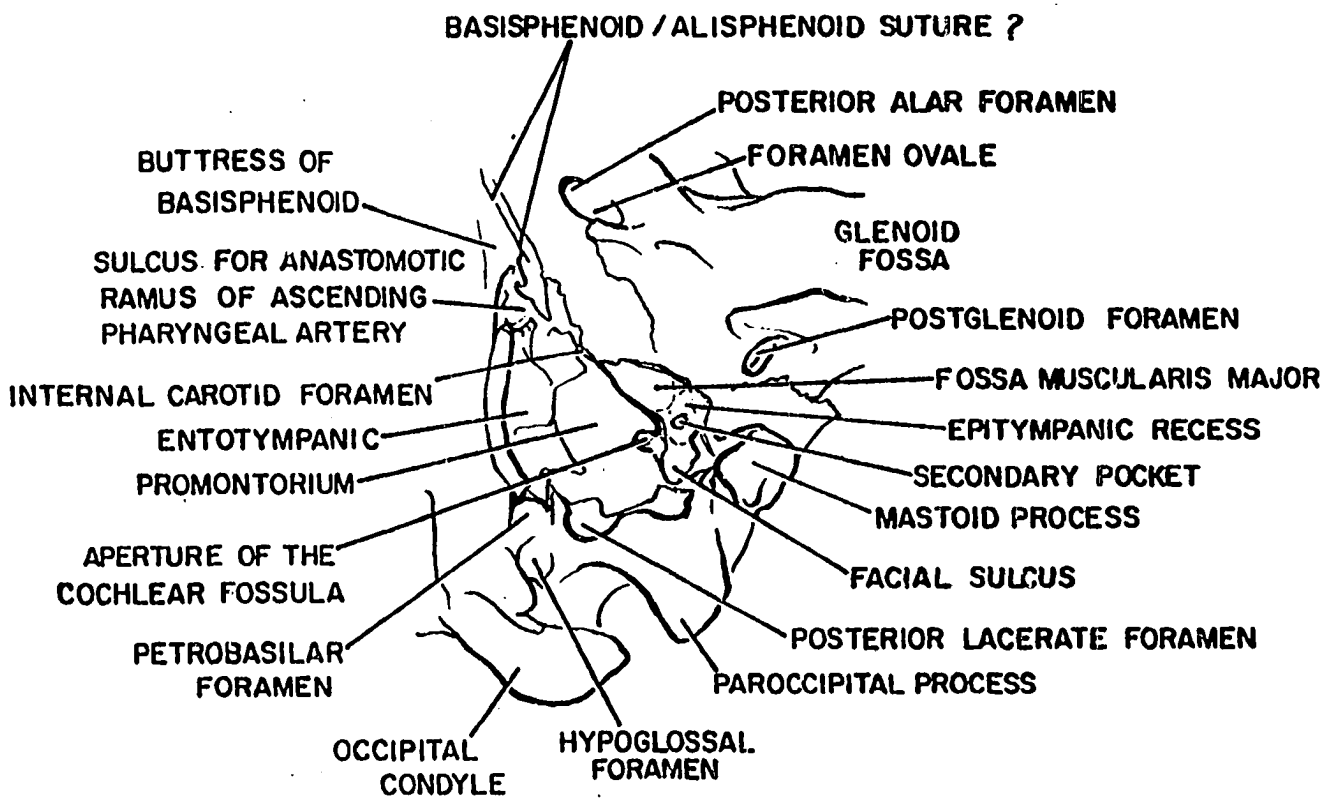


Figure 32: Stereo pair of the right auditory region of Dinictis sp., F:AM 62034, posterolateral and slightly ventral view.

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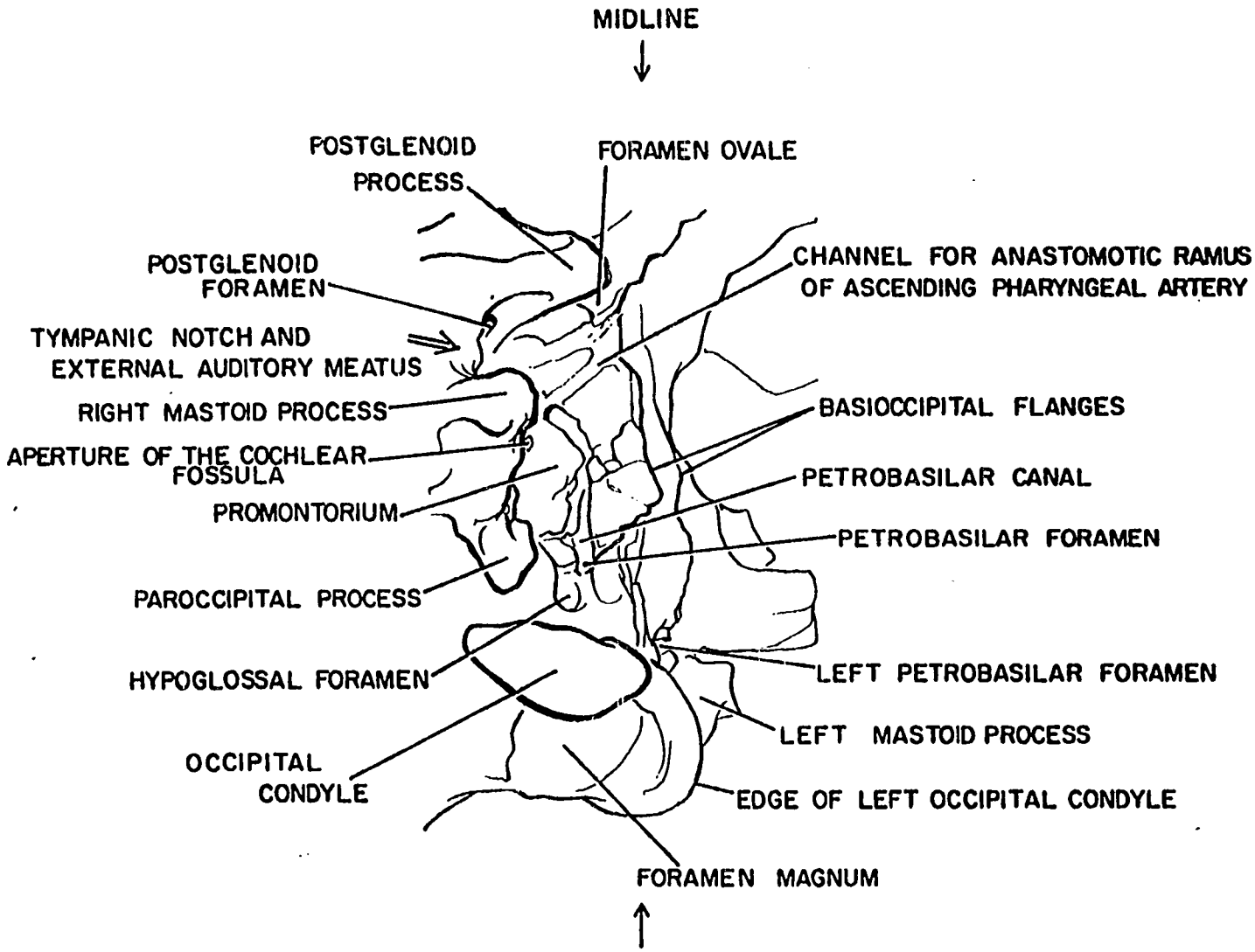
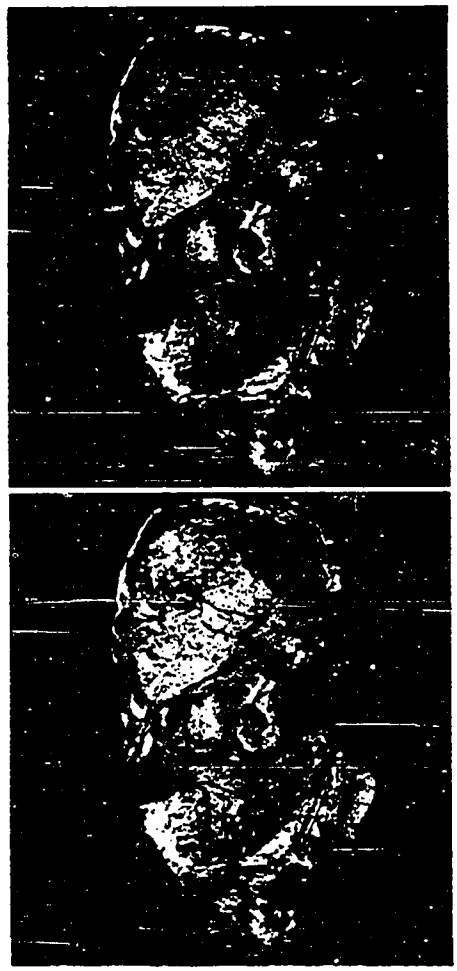
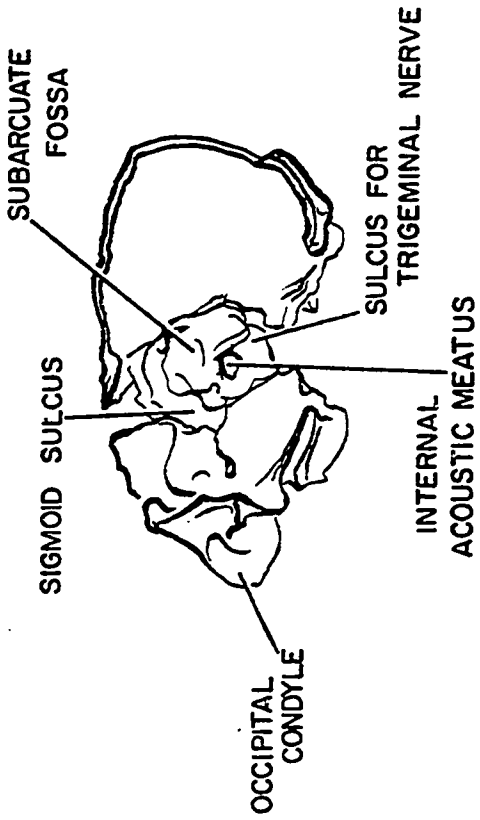


Figure 33: Stereo pair of the intracranial aspect of the left otic region of Dinictis, AMNH SD 230-4152, anteromedial view.

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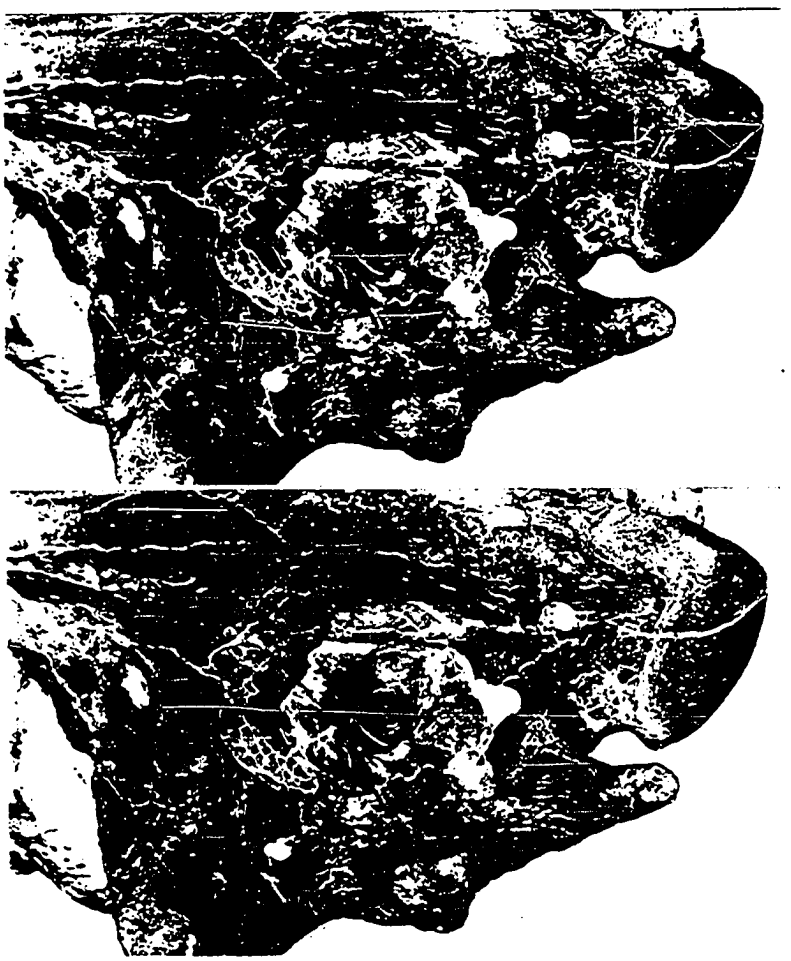
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Figure 34: Stereo pair of the right auditory region of Nimravus brachyops, YPM 14385, showing anterior accessory sinus. Ventral view.

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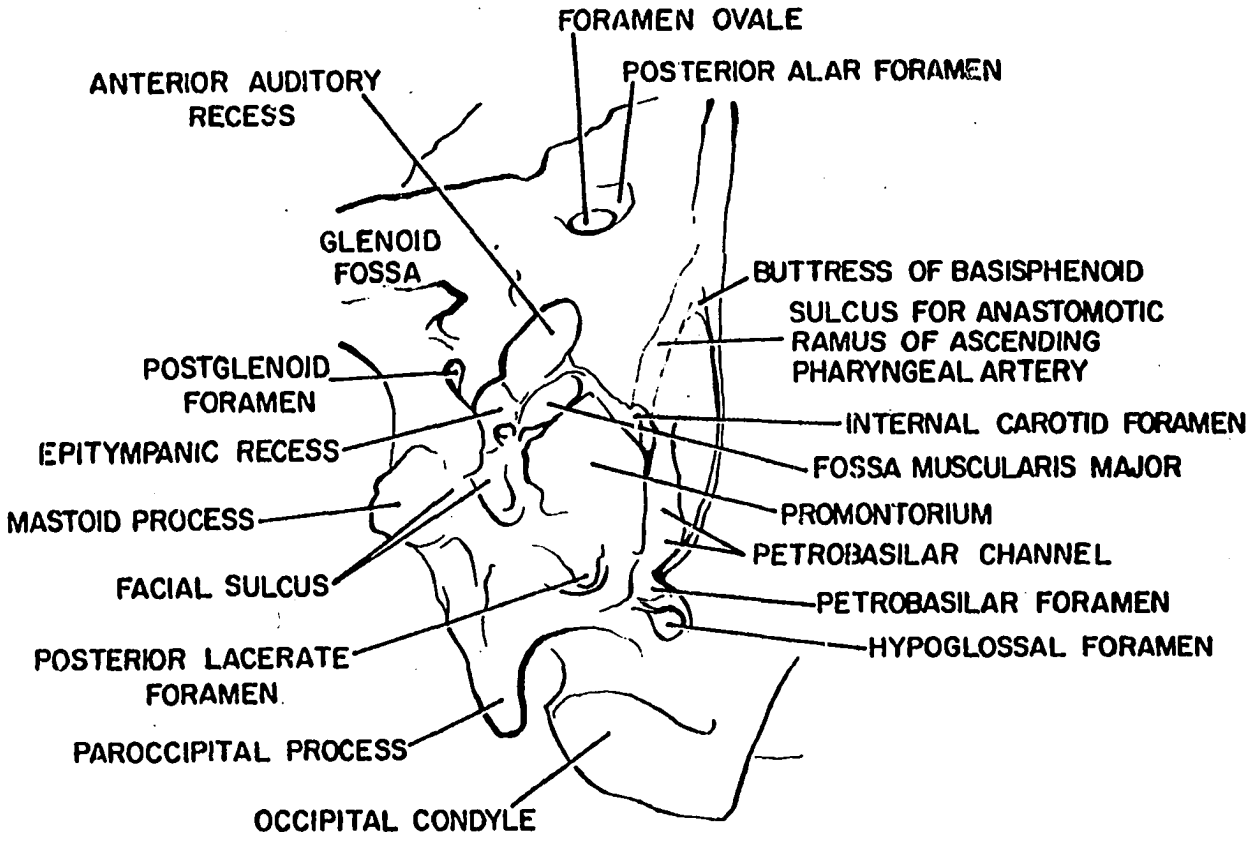
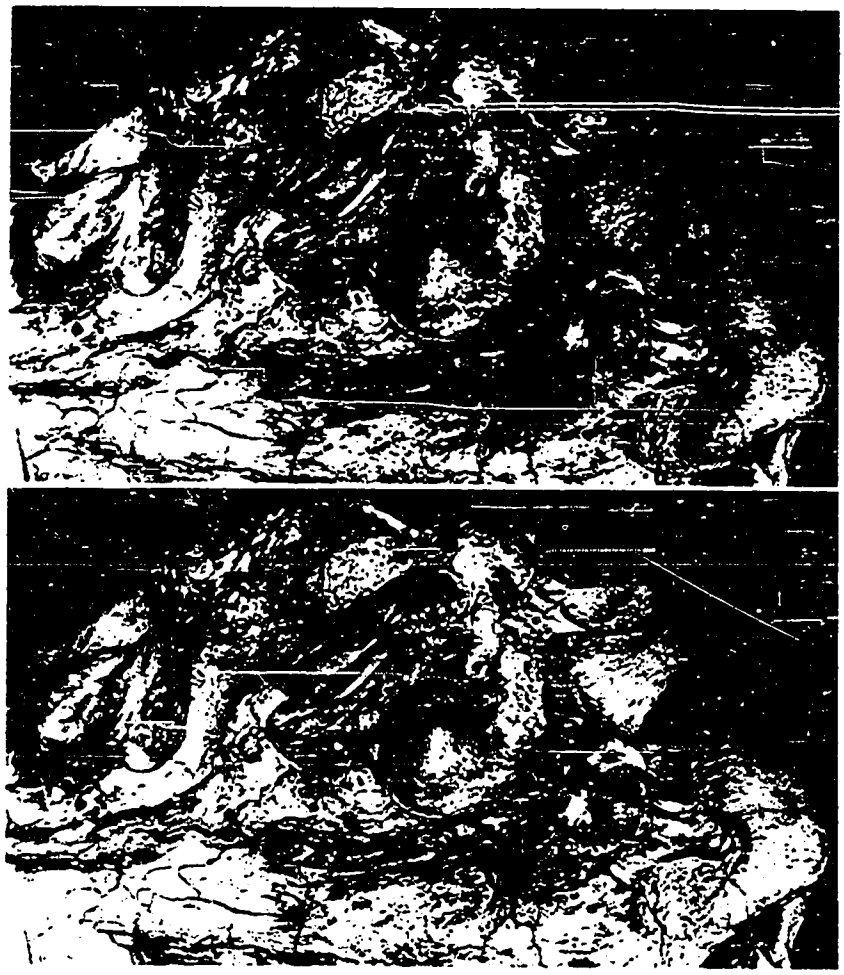
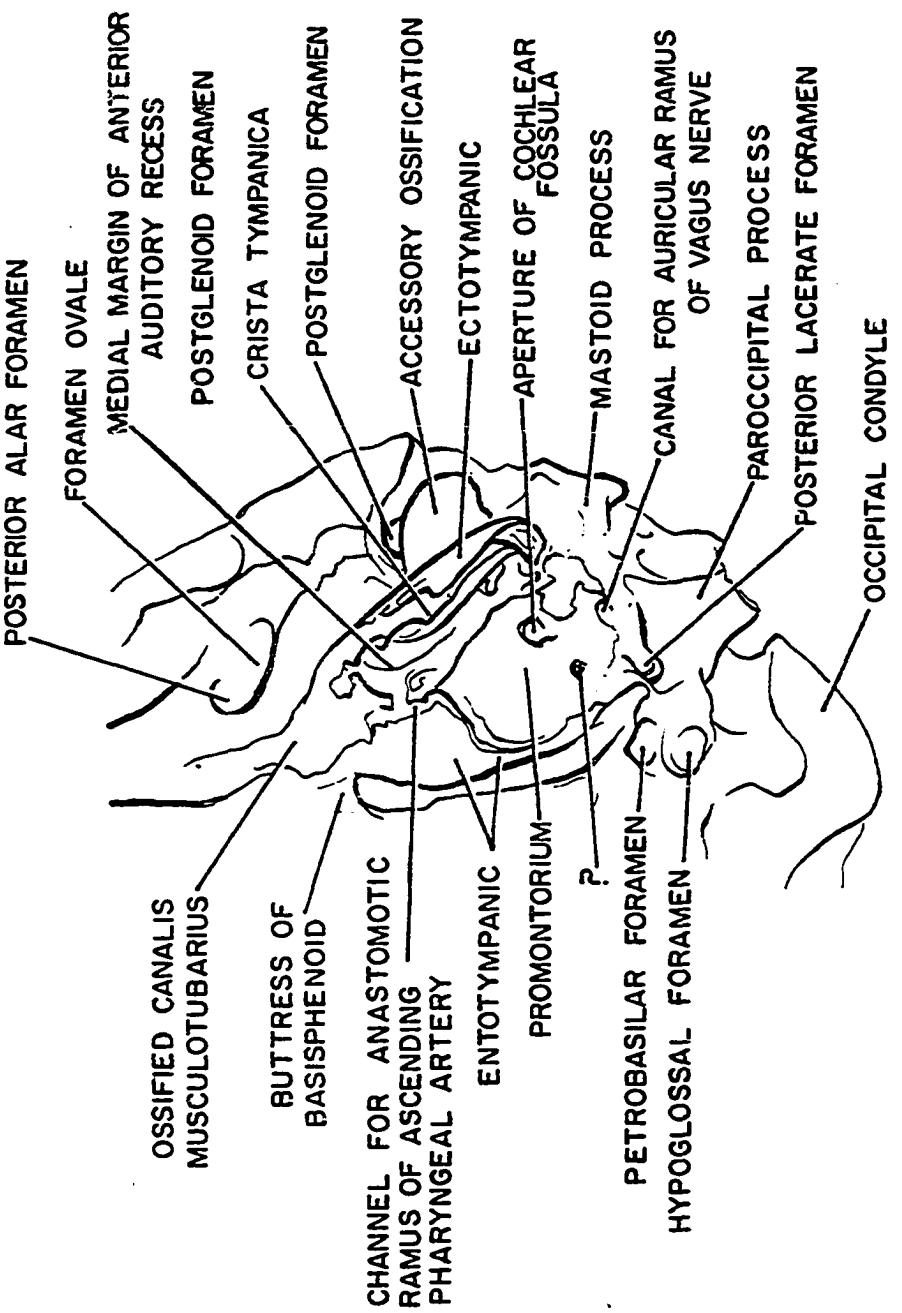


Figure 35: Stereo pair of the left auditory region of Nimravus sp., F:AM 62020, ventral view. The extra accessory ossification in the anteroventral wall of the external auditory meatus is in place in this specimen.

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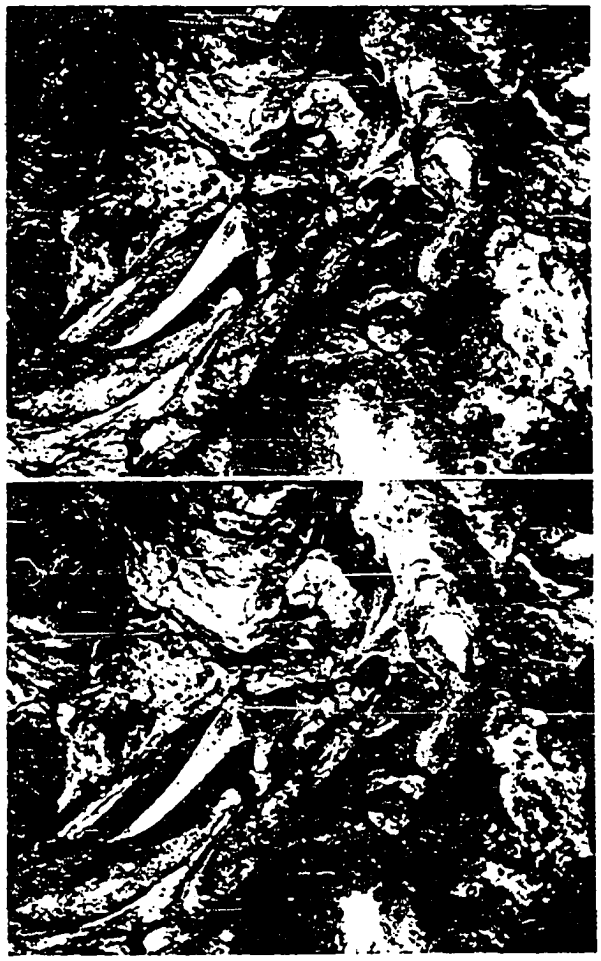
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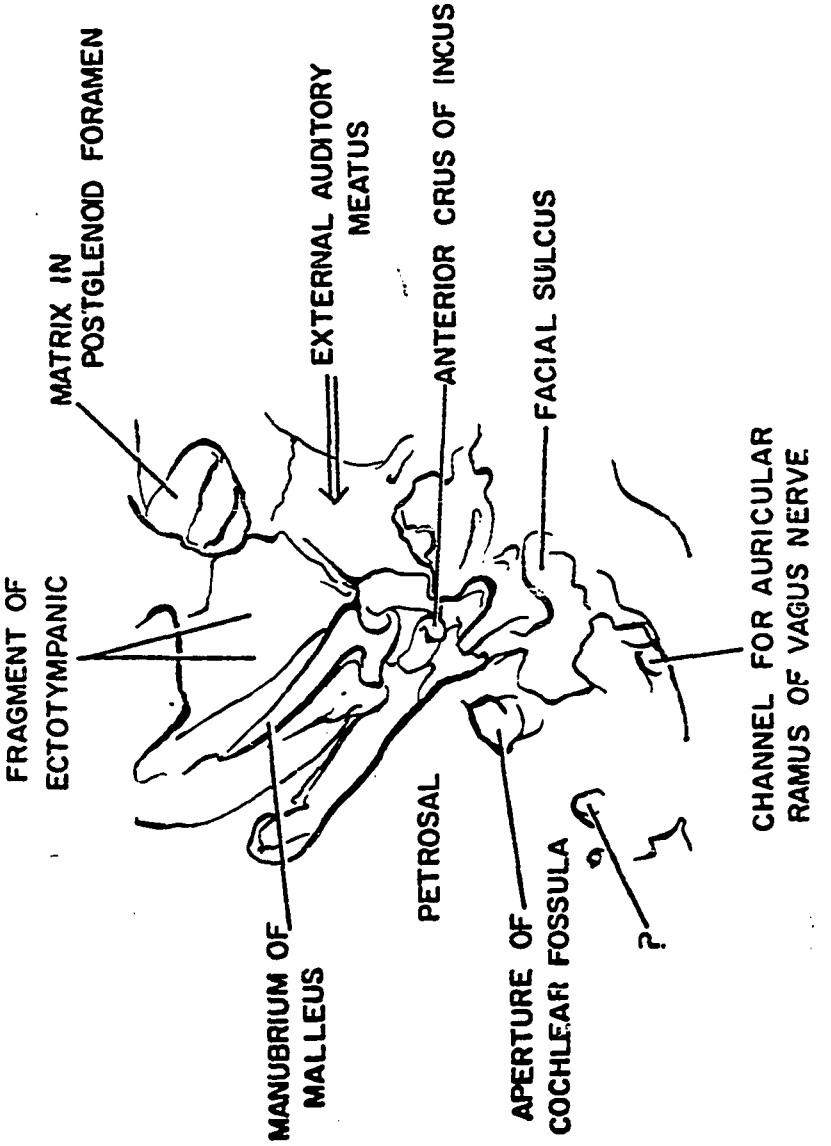
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Figure 36: Stereo pair of a detail of the same auditory region shown in Figure 35, showing the manubrium and neck of the malleus and anterior crus of the incus of Nimravus sp., F:AM 62020.

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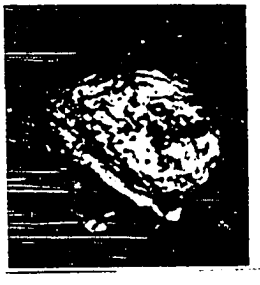
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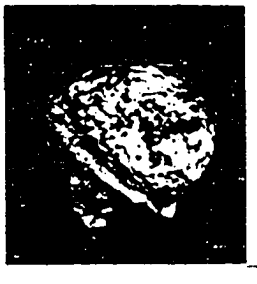
Figure 37: Stereo pairs presenting A) dorsal and B) ventral views of the accesscry ossification from the external auditory meatus of Nimravus sp., F:AM 620920.

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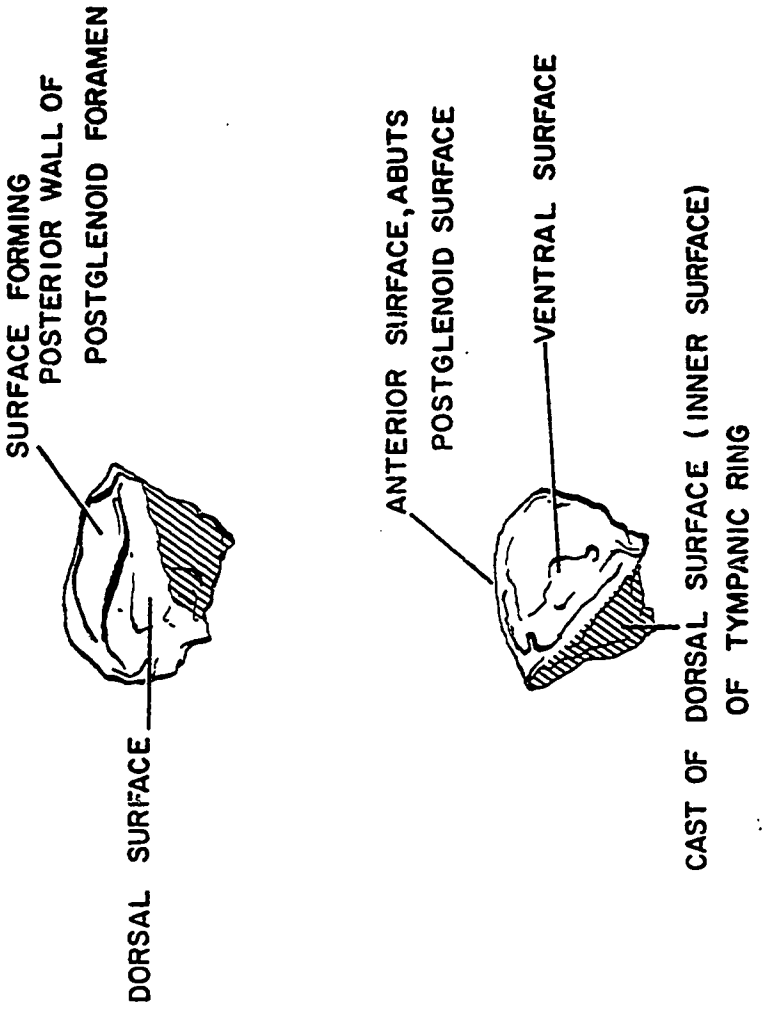








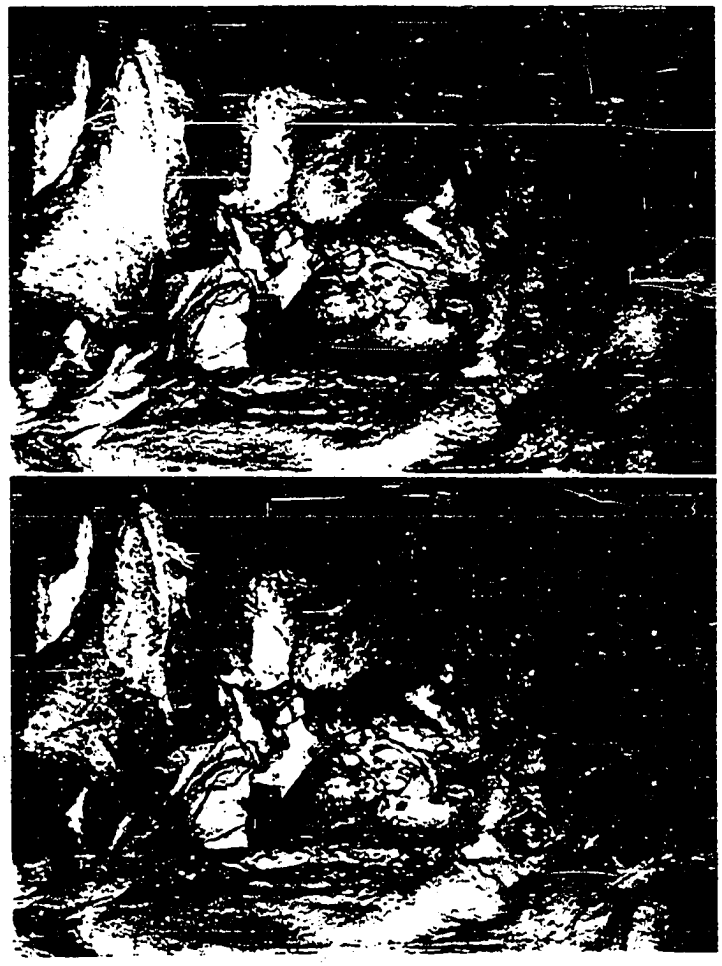
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Figure 38: Stereo pair of the left auditory region of Hoplophoneus sp., AMNH 82440, ventral view, showing the canal in the posterior part of the entotympanic, hypothesized here to have conveyed a laterally positioned internal carotid artery (="promontory artery").

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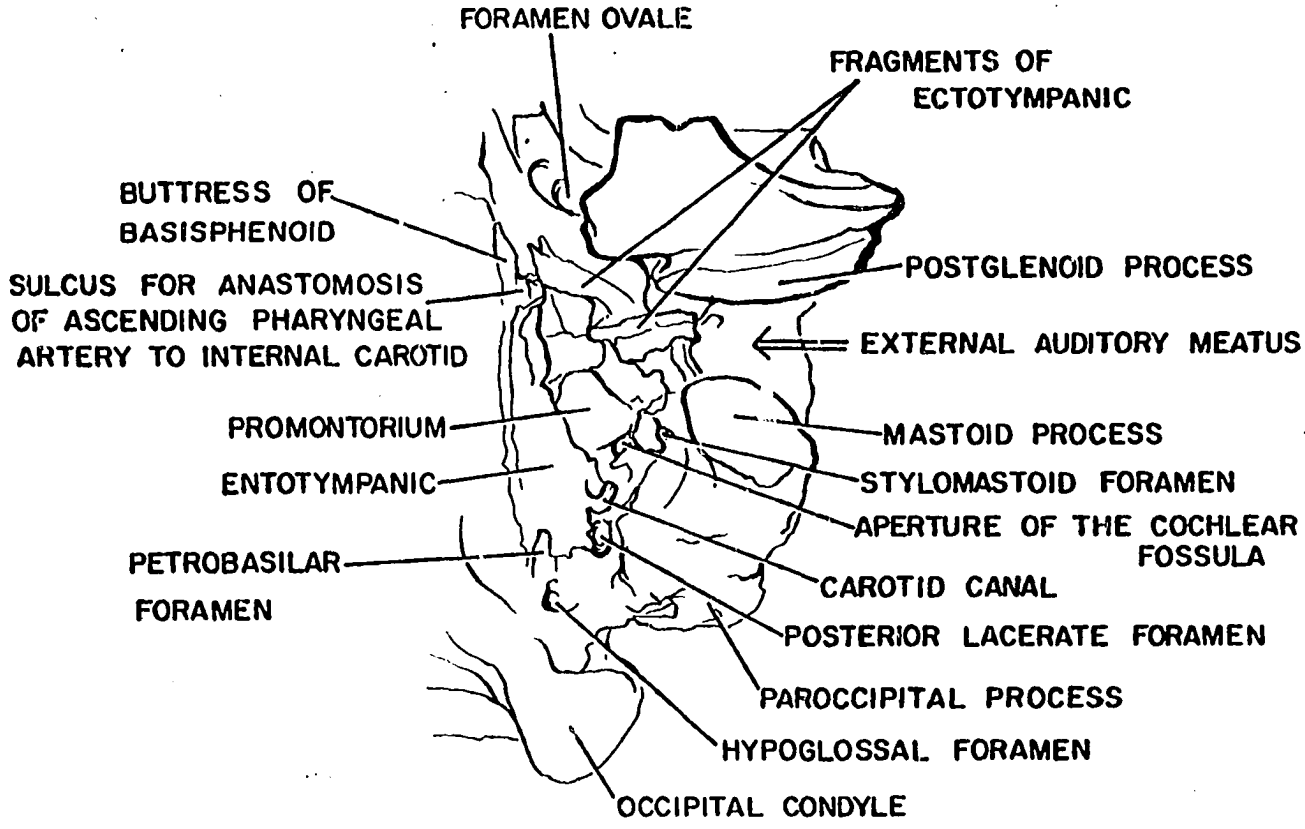


Figure 39: Stereo pair of the intracranial anatomy of the left otic region of Hoplophoneus sp., AMNH 82440, medial and slightly anterior view.

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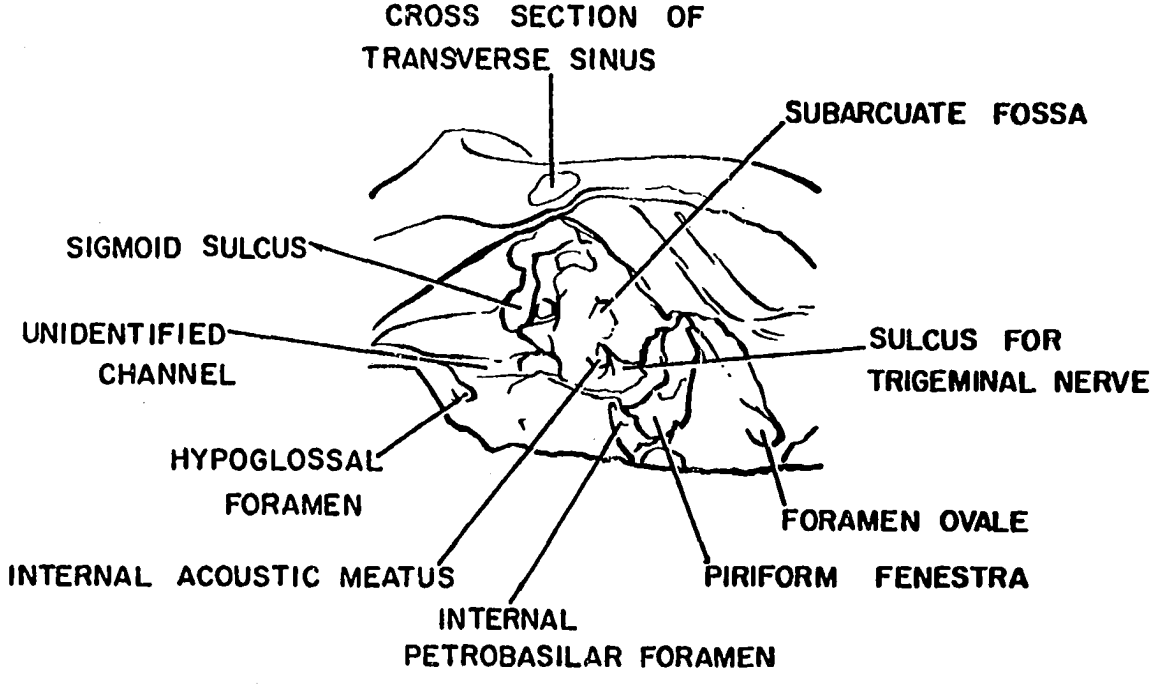
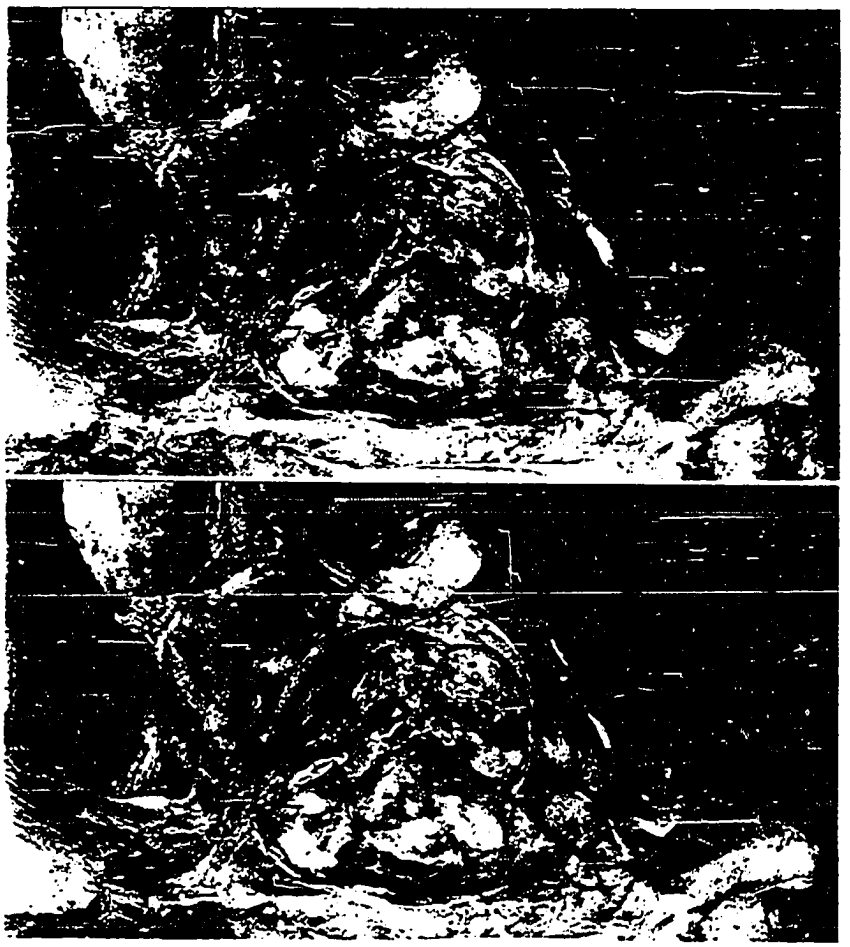
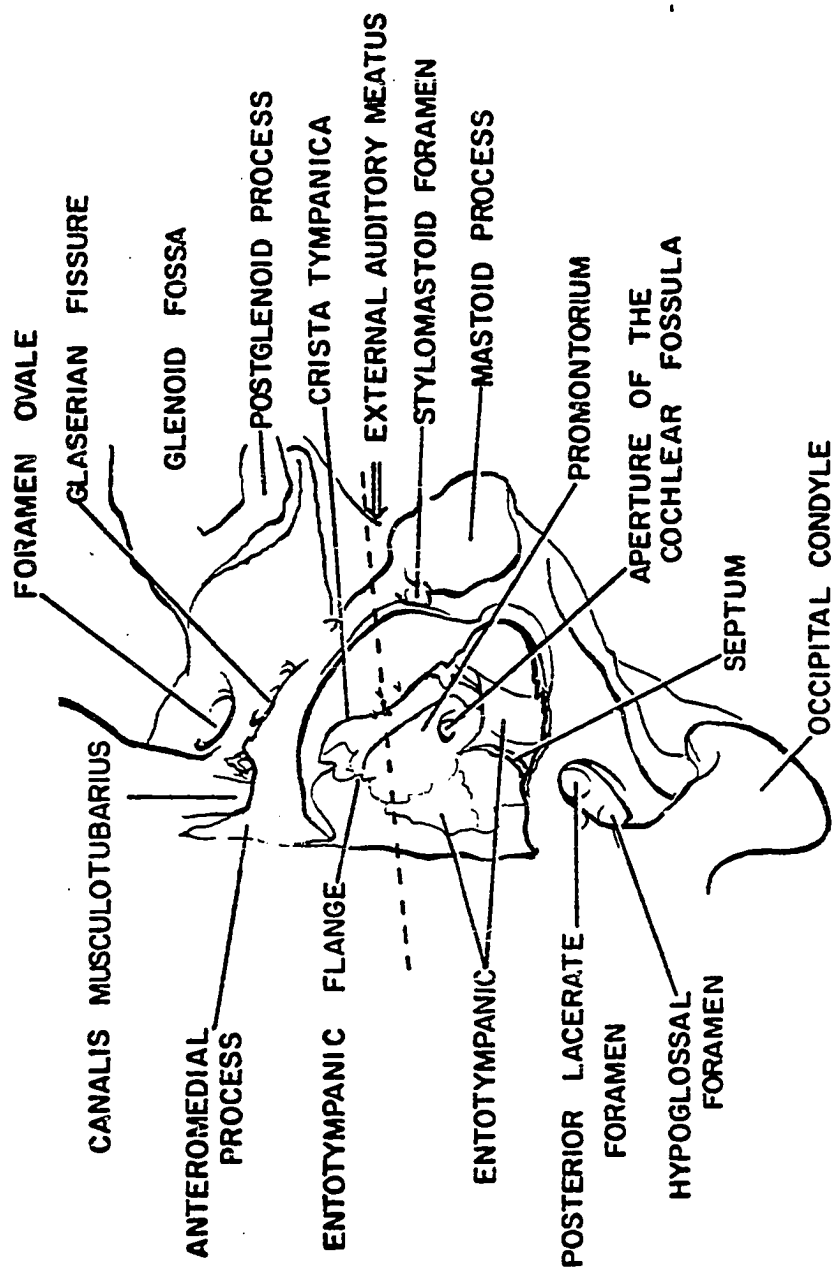


Figure 40: Stereo pair of the left auditory region of Barbourofelis morrisi, F:AM 61871, ventral view. The ventral portion of the bulla is broken in this specimen so that some of the tympanic roof and intrabullar structures are visible.

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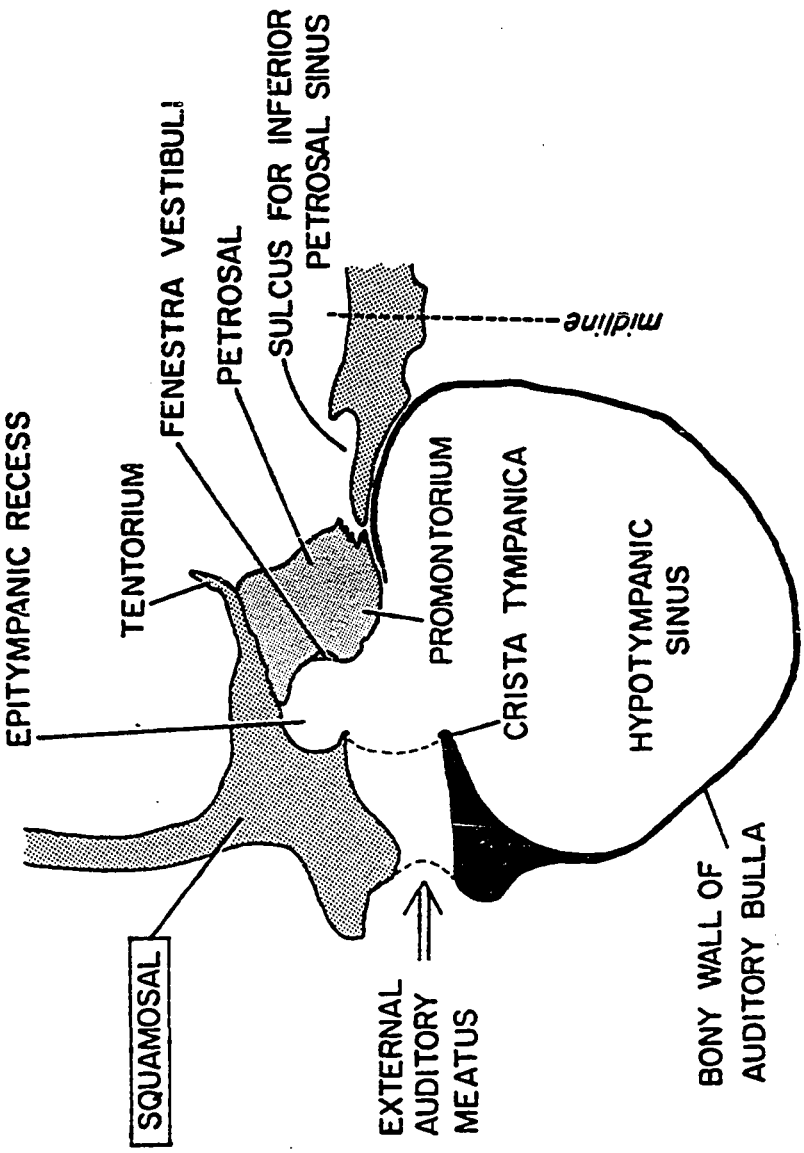
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Figure 41: Diagrammatic cross section through the auditory region of Barbourofelis, at approximately the level indicated in the diagram accompanying Figure 40. Based generally on F:AM 61871 and UF 36867.

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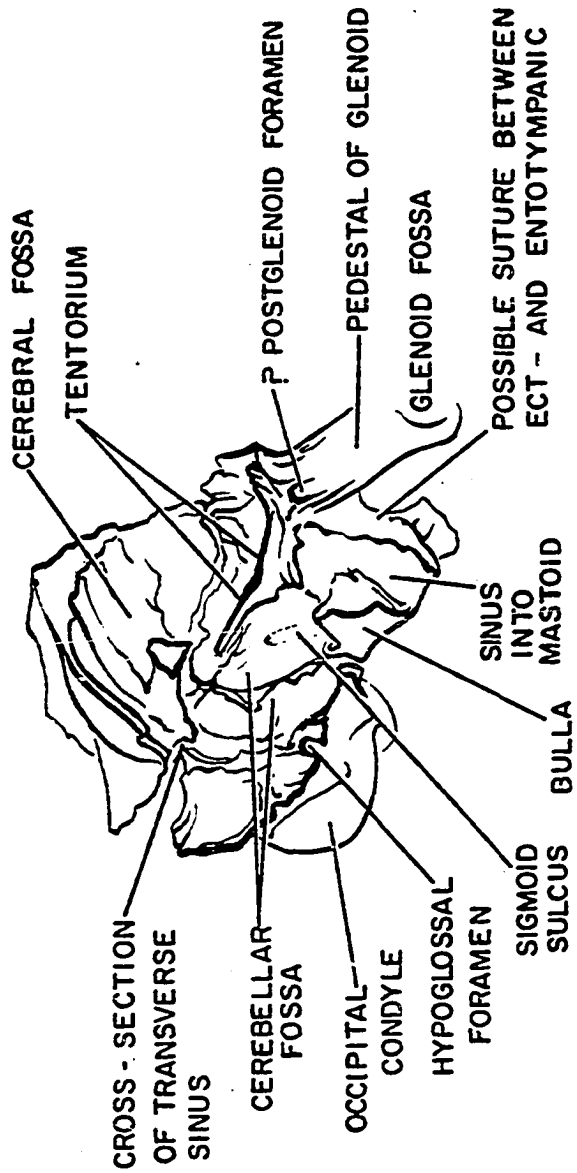
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Figure 42: Stereo pair of the intracranial anatomy of the left otic region and posterior portion of the skull of Barbourofelis morrisi, F:AM 61961, anteromedial view.

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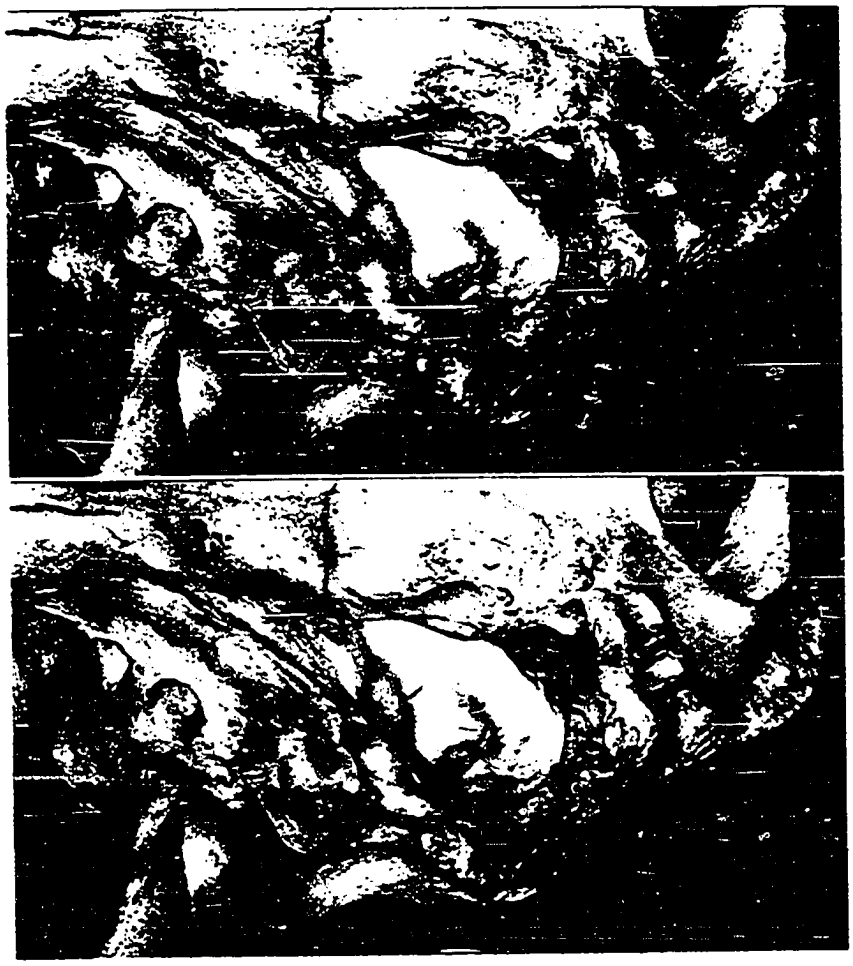
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Figure 43: Stereo pair of the auditory region of *Felis catus*, AMNH AINS:589, ventral view, bulla removed.

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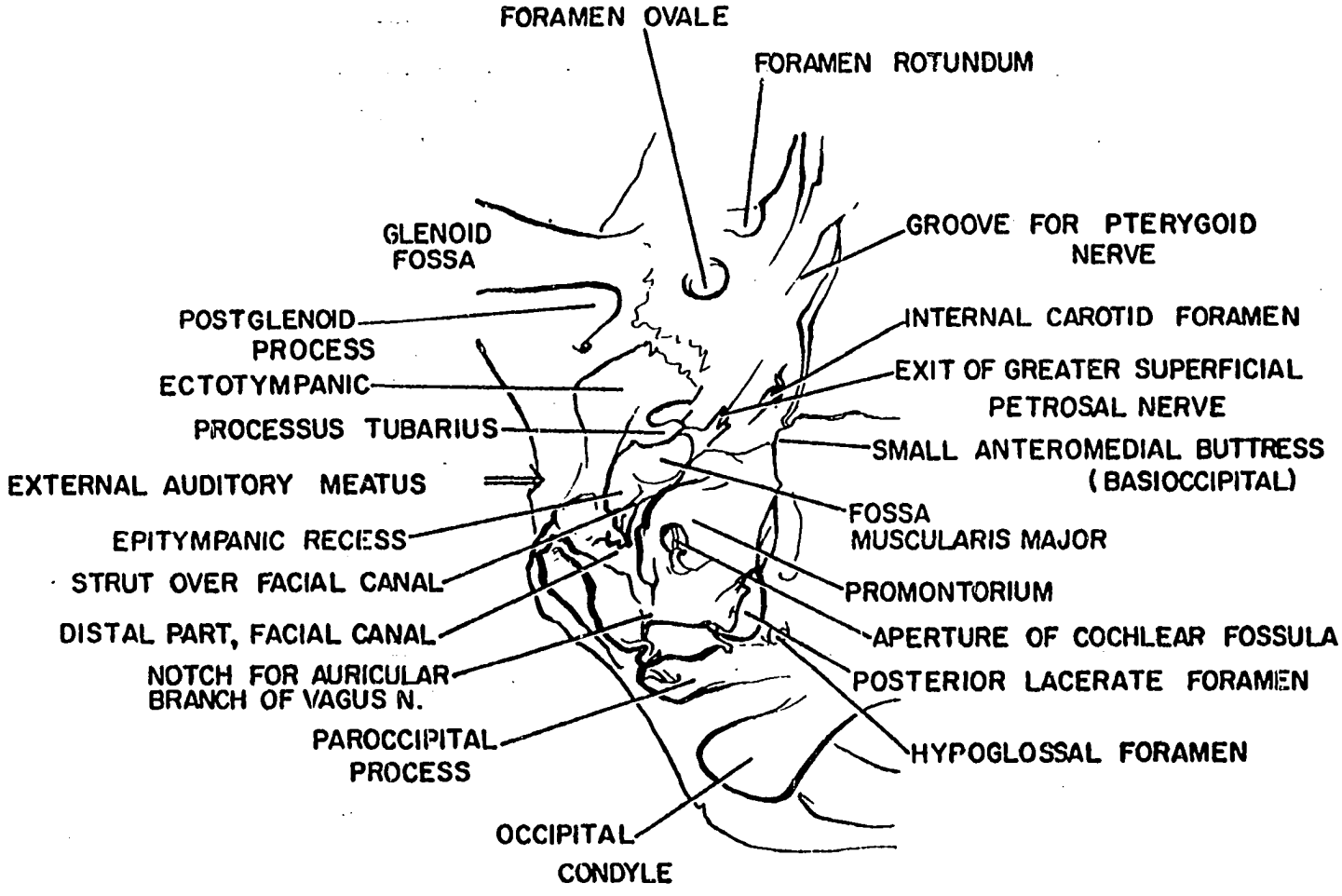
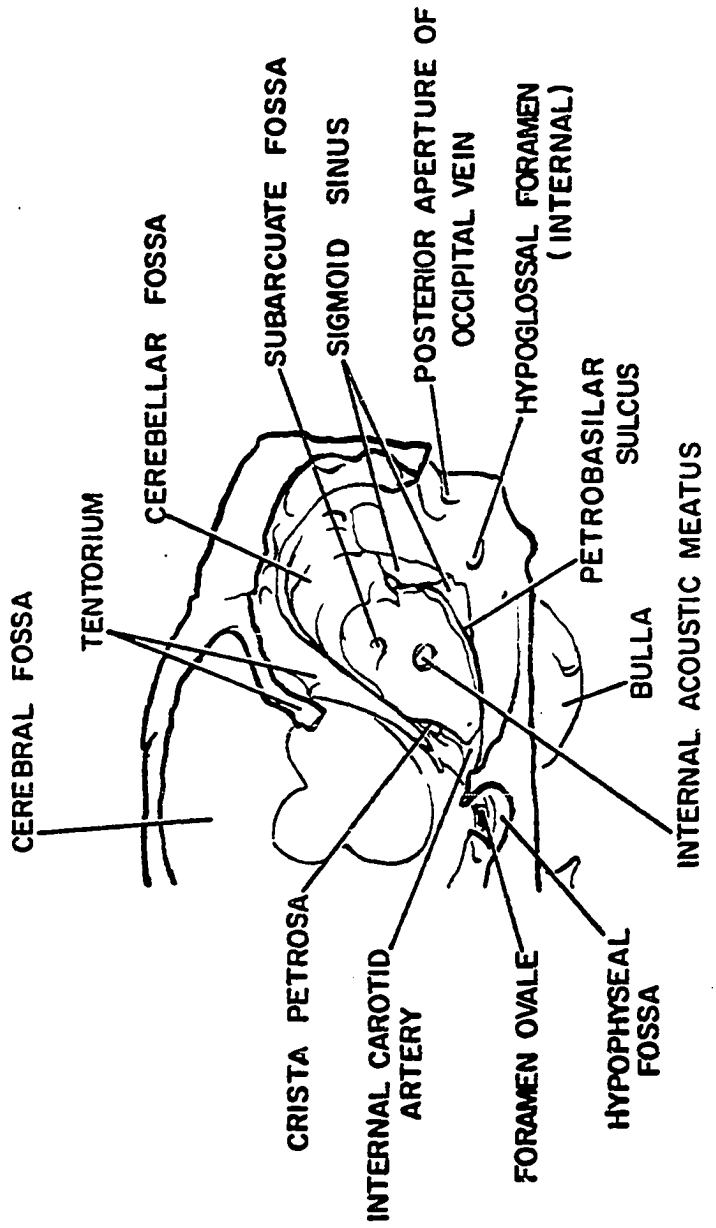


Figure 44: Stereo pair of the intracranial features in the right otic region of the skull of Felis catus, AMNH uncatalogued.

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Figure 45: Stereo pair of the left auditory region of Pseudaelurus sp., F:AM 61835, ventral view. The ventral wall of the bulla is broken away, and a window broken in the septum, revealing the anterior chamber.

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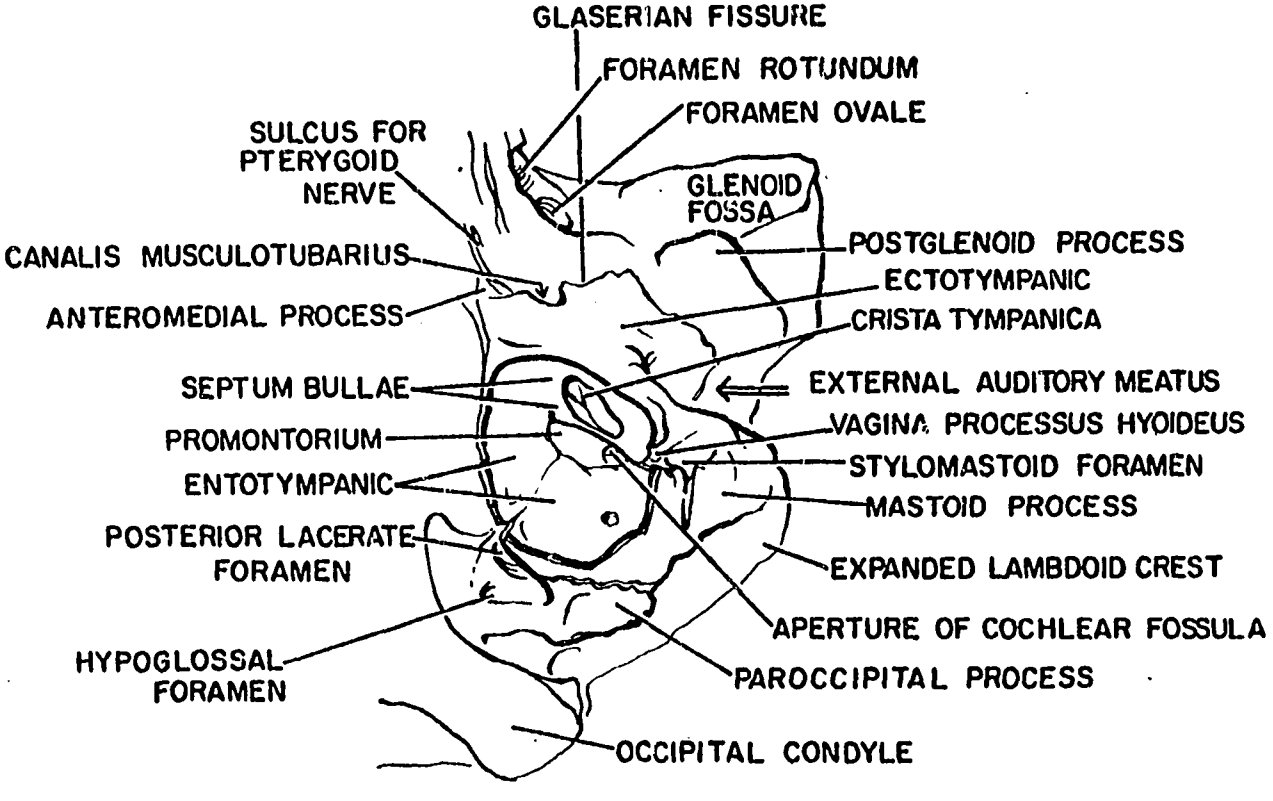
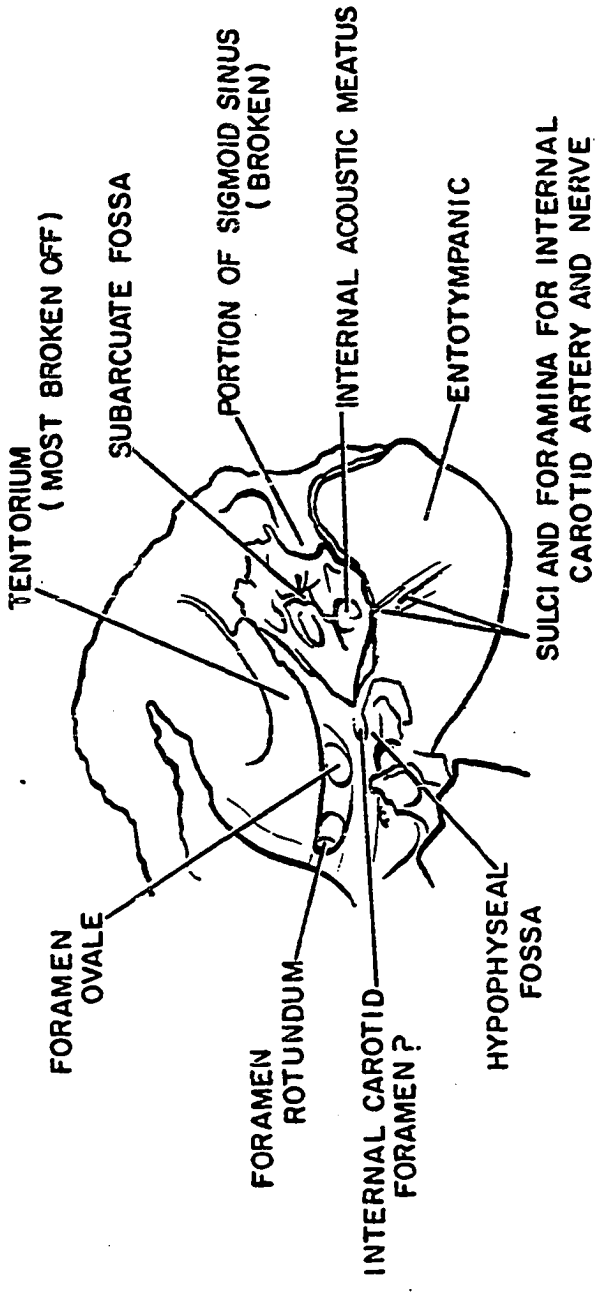


Figure 46: Stereo pair of the intracranial surface of the right otic region and medial surface of the auditory bulla of *Smilodon floridanus*, LACM HC7000.

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Figure 47: Anterior view of a diagrammatic cross section of the basicranium of Felis catus, sliced at a slight angle so that the section of the specimen's left side is more anterior than that of the right side. As a result, a large portion of the fossa muscularis major is visible on the left side, and only a small part on the right, while on the latter side the epitympanic recess, slightly posterior, is clearly bisected. The vertical hatching denotes a sectioned surface.

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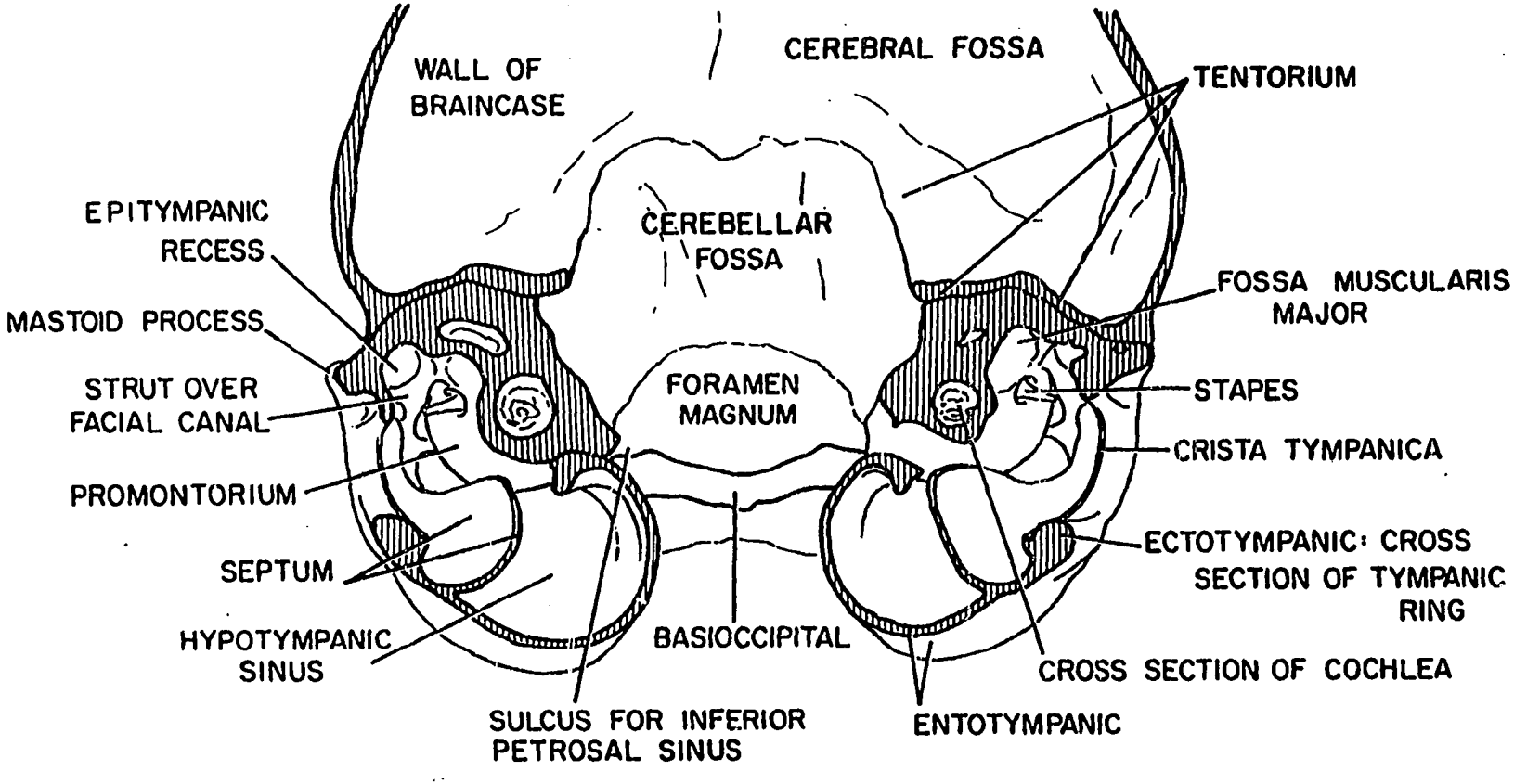
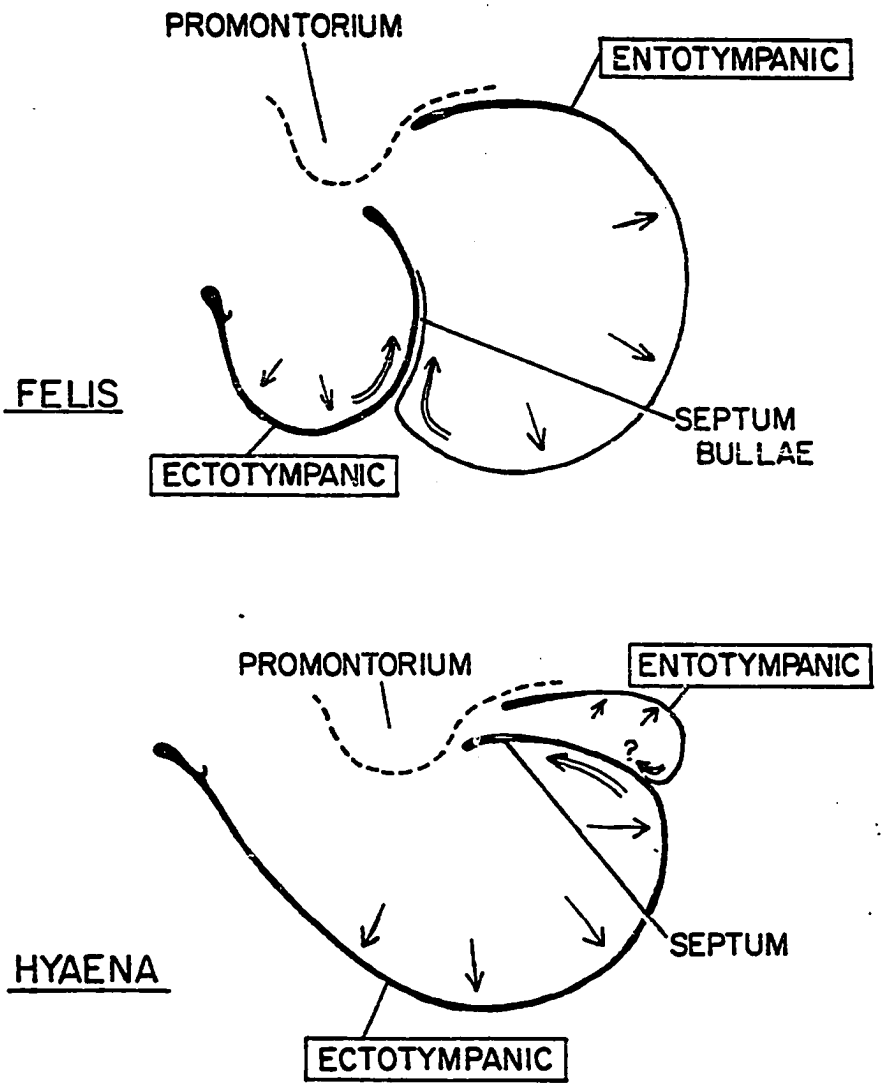


Figure 48: Diagrams contrasting the relative amounts of inflation of the ento- and ectotympanic portion of the bulla in *Felis* and *Hyaena*.

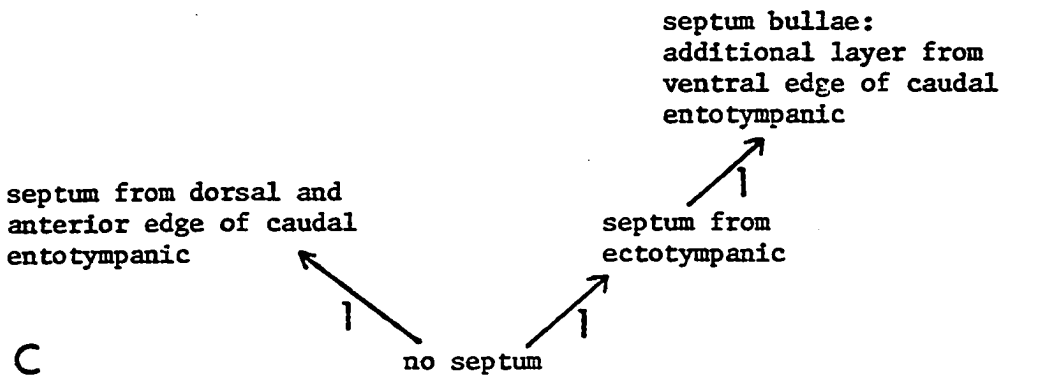
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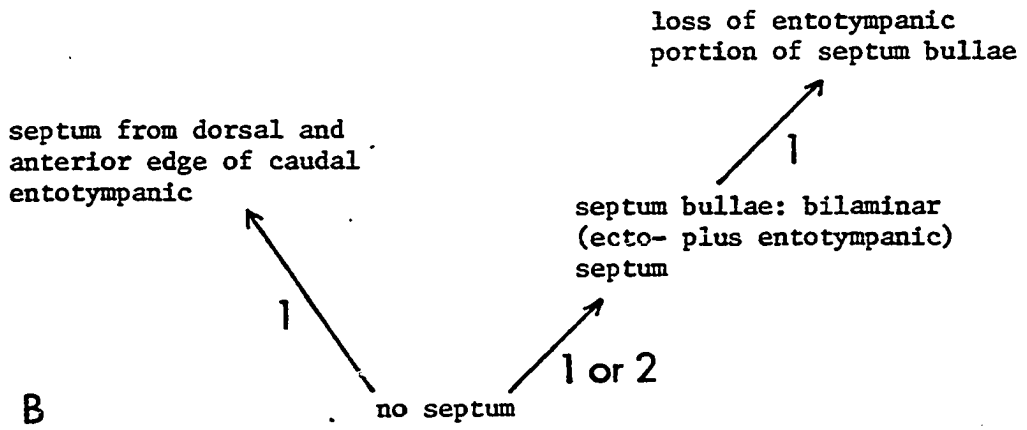


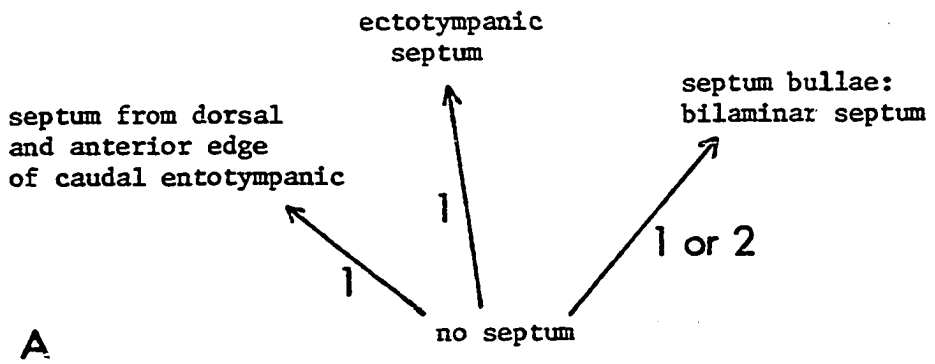
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Figure 49: Three character state trees for the various septa recognized within the Carnivora.

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Figure 50: Stereo pair of the left auditory region of Canis latrans, AMNH AINS:668-B, ventral view, showing the anterior entotympanic septum.

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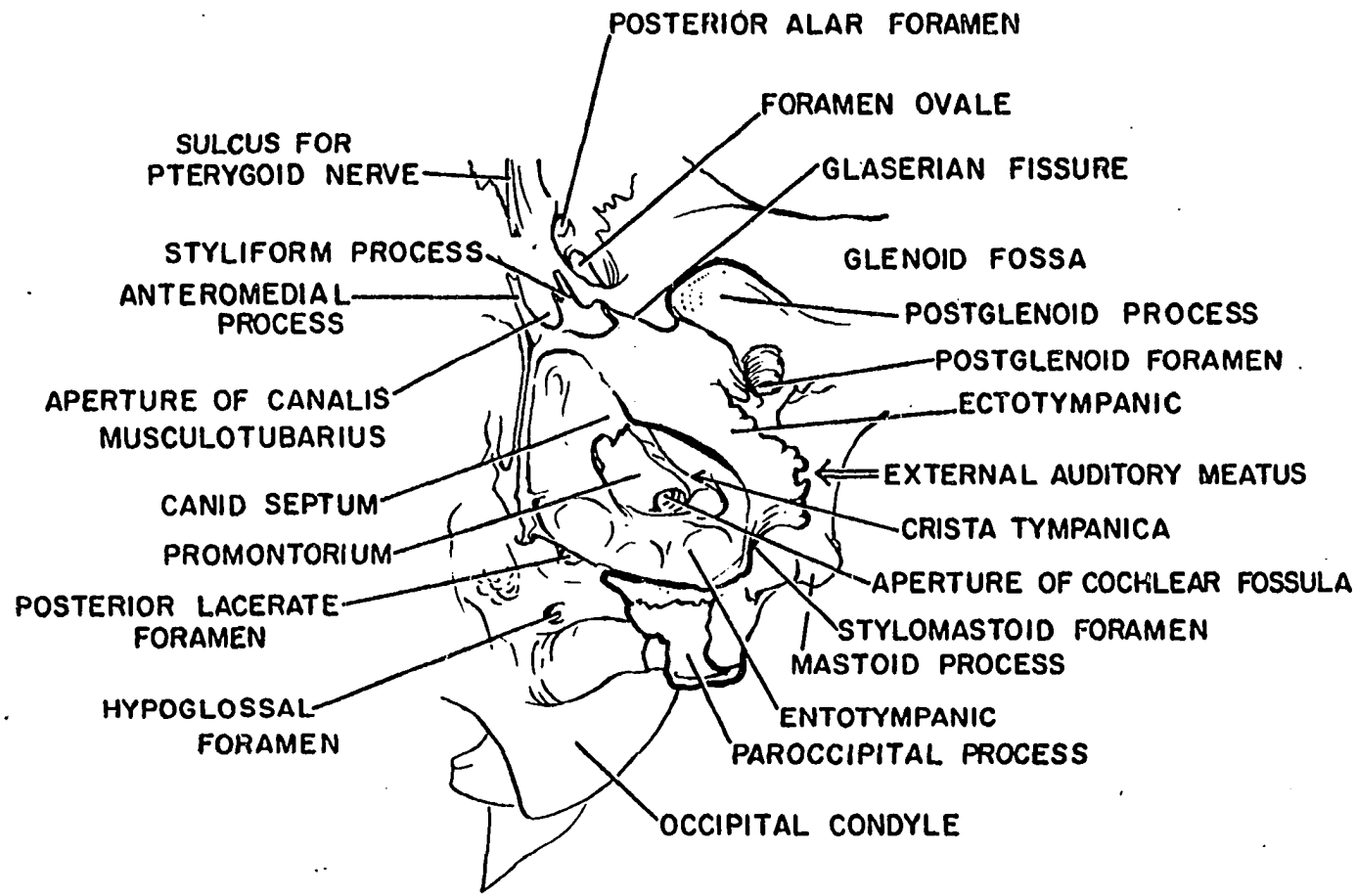
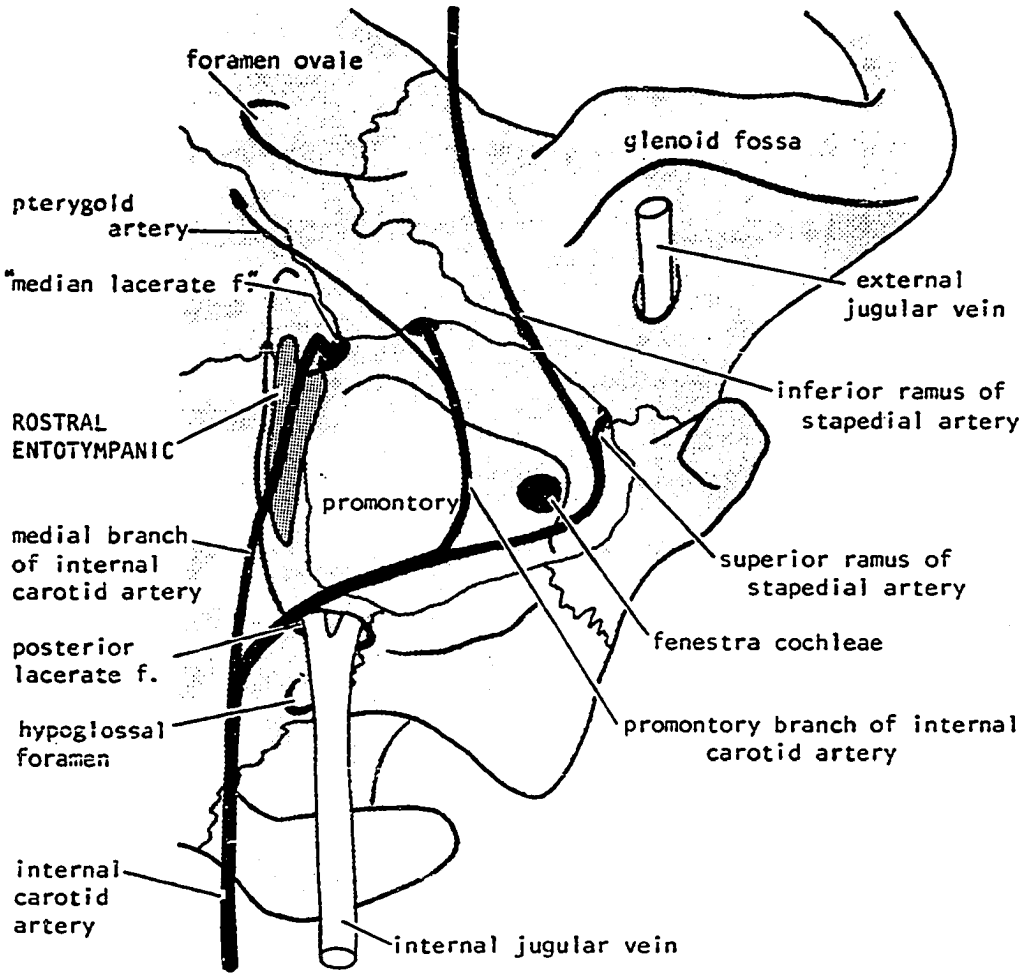


Figure 51: A diagrammatic summary of Matthew;s (1909) hypothesis of the primitive carotid pattern and the morphotype used by subsequent authors. The relationship with the rostral entotympanic is from Hunt (1974a), although the position of the artery so far medially was earlier proposed by Matthew.

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Figure 52: Four transverse sections through the ear region of various mammals, redrawn from Presley (1979), showing the development of the internal carotid artery. Midline is at the left of each section; stippled area is developing bone; dark stipple is ectotympanic; double-walled white vessel below promontorim is dorsal aorta or internal carotid artery; solid black denotes nerves.

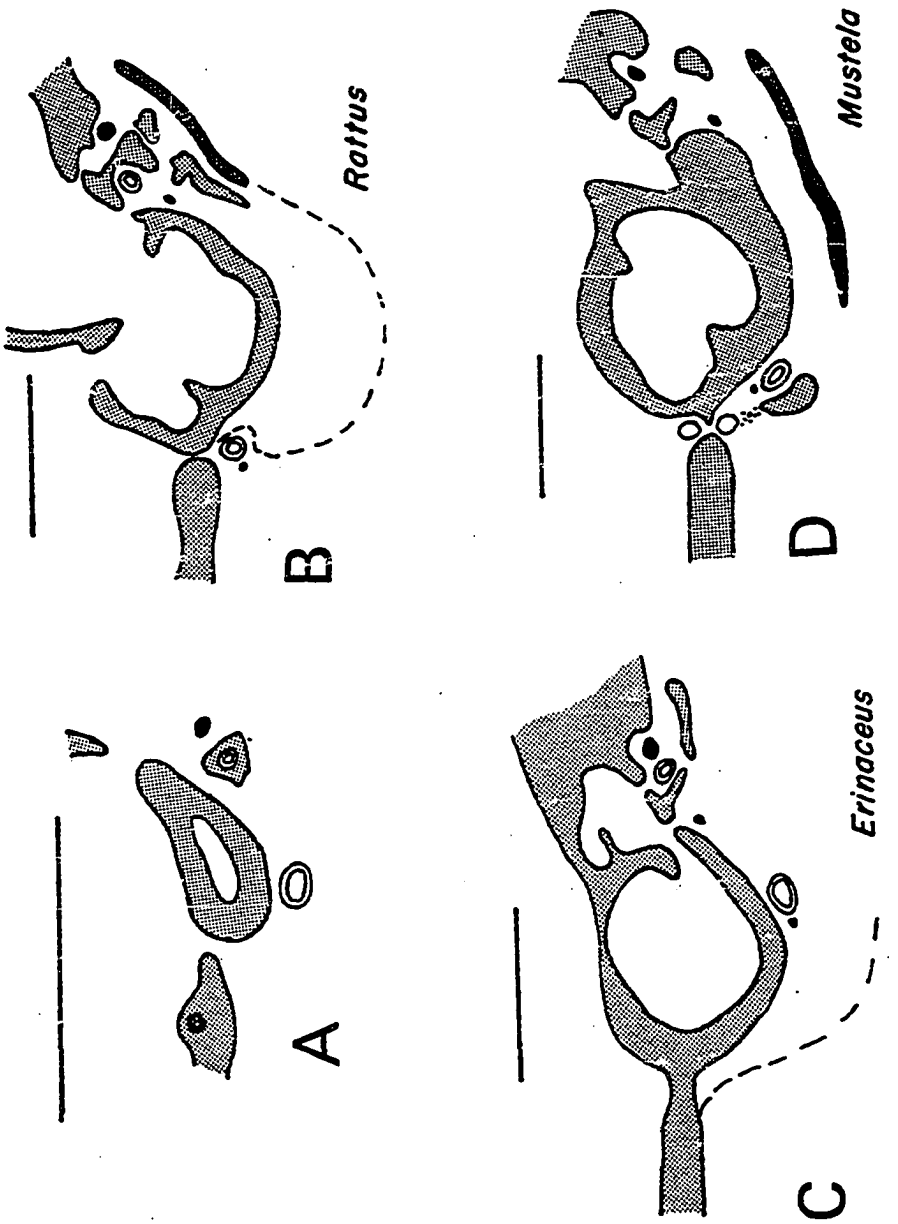
A: Early embryo, generally typical of all mammals. Rattus norvegicus, 12 mm CRL.

B: Later stage of mammal with medial branch of internal carotid artery; future extent of ectotympanic bulla indicated by dashed line. Rattus norvegicus newborn.

C: Later stage of mammal with promontory branch of internal carotid artery; dashed line indicates future extent of basisphenoid wing. Erinaceus europaeus, 13 mm HL.

D: Later stage of carnivoran, with medial branch of internal carotid lateral to developing entotympanic. Mustela domestica, newborn.

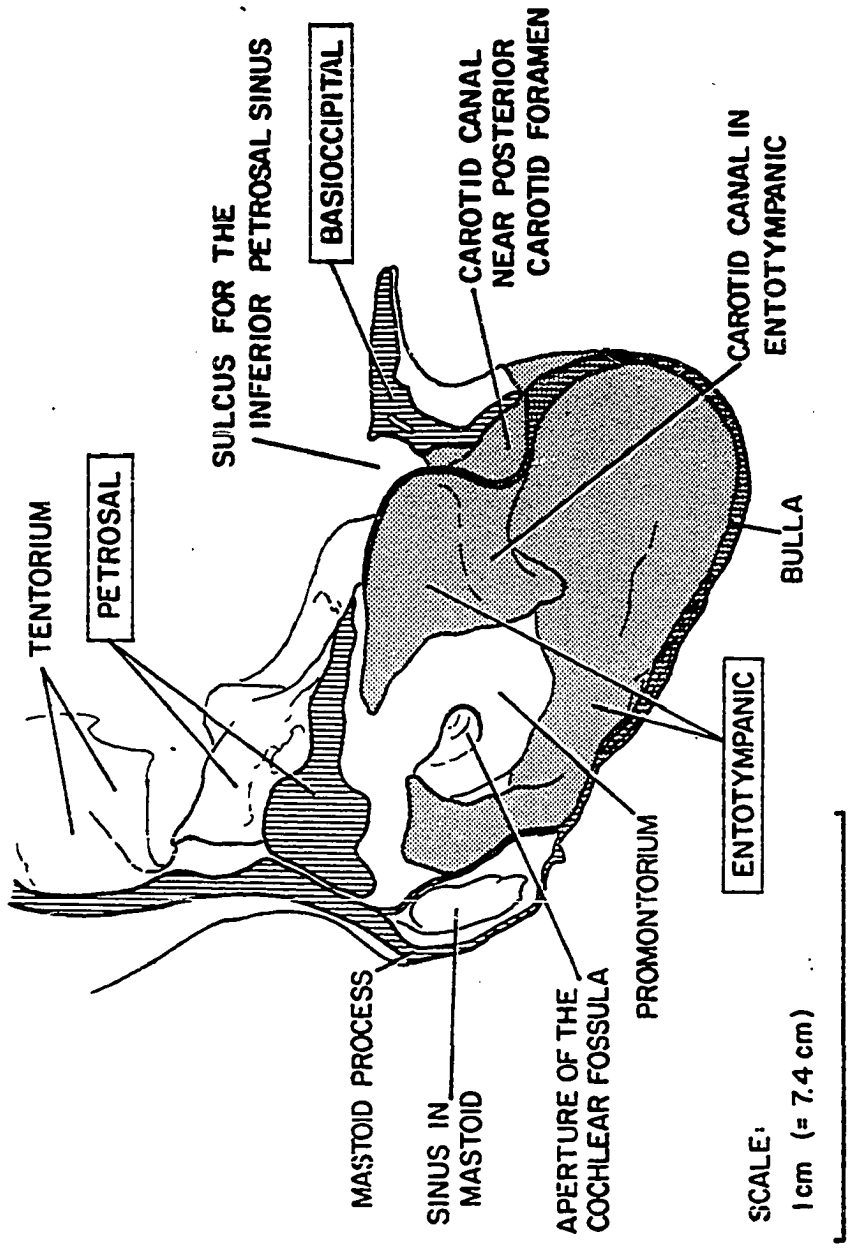
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Figure 53: Cross sections at two levels through the left basicranium of Viverra sp., AMNH CA 1709. A) Posterior aspect of the sectioned basicranium at the level of the posterior carotid foramen. B) Posterior aspect of the same basicranium sectioned more anteriorly, at the level of the anterior end of the entotympanic. The bulla, both ecto- and entotympanic, is shaded in both drawings; the vertical hatching denotes a sectioned surface.

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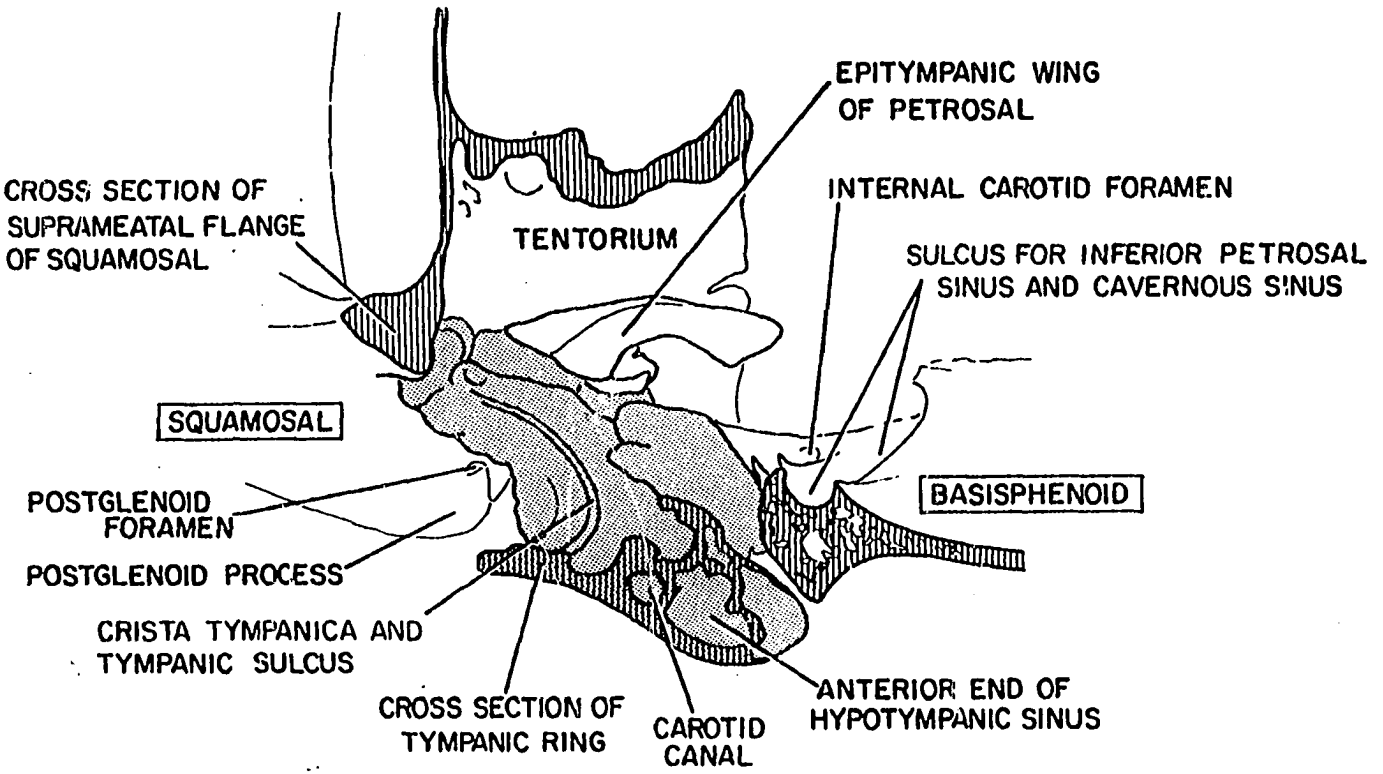
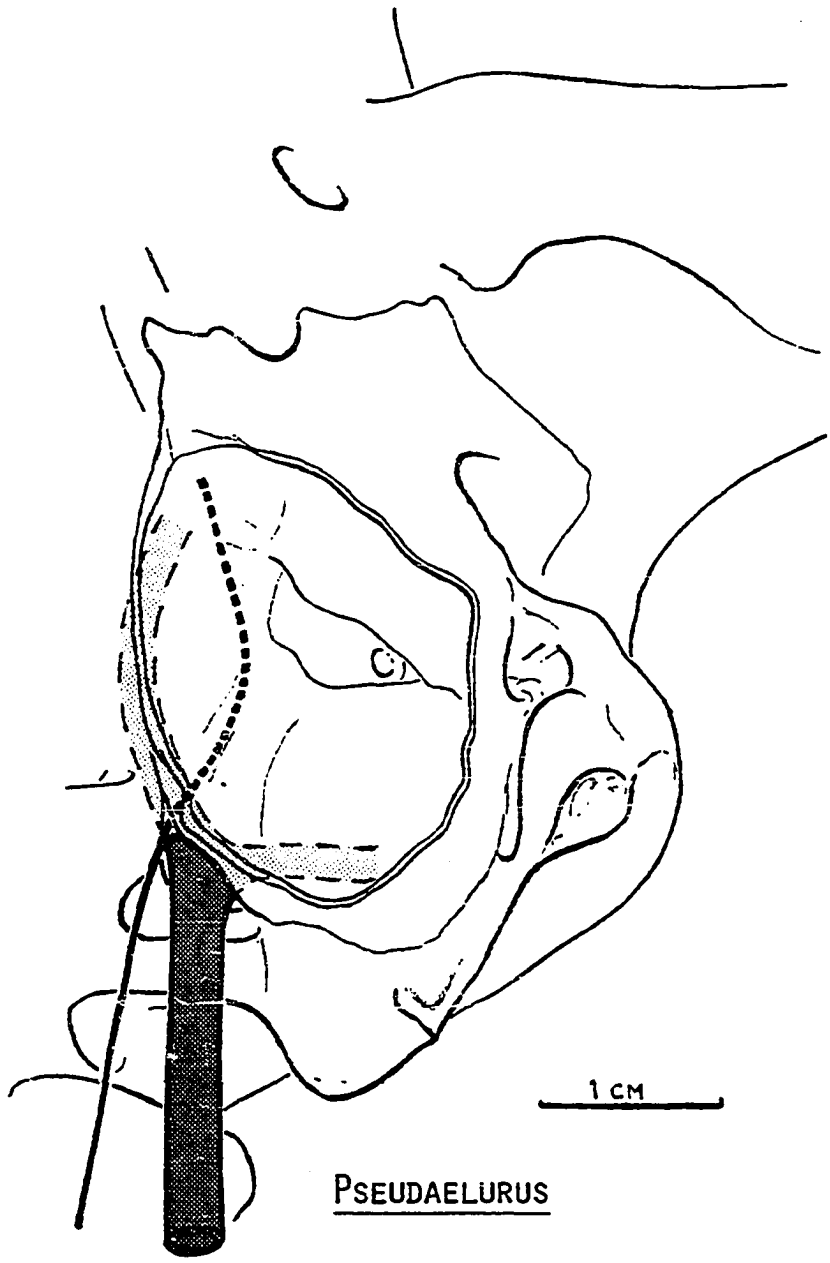


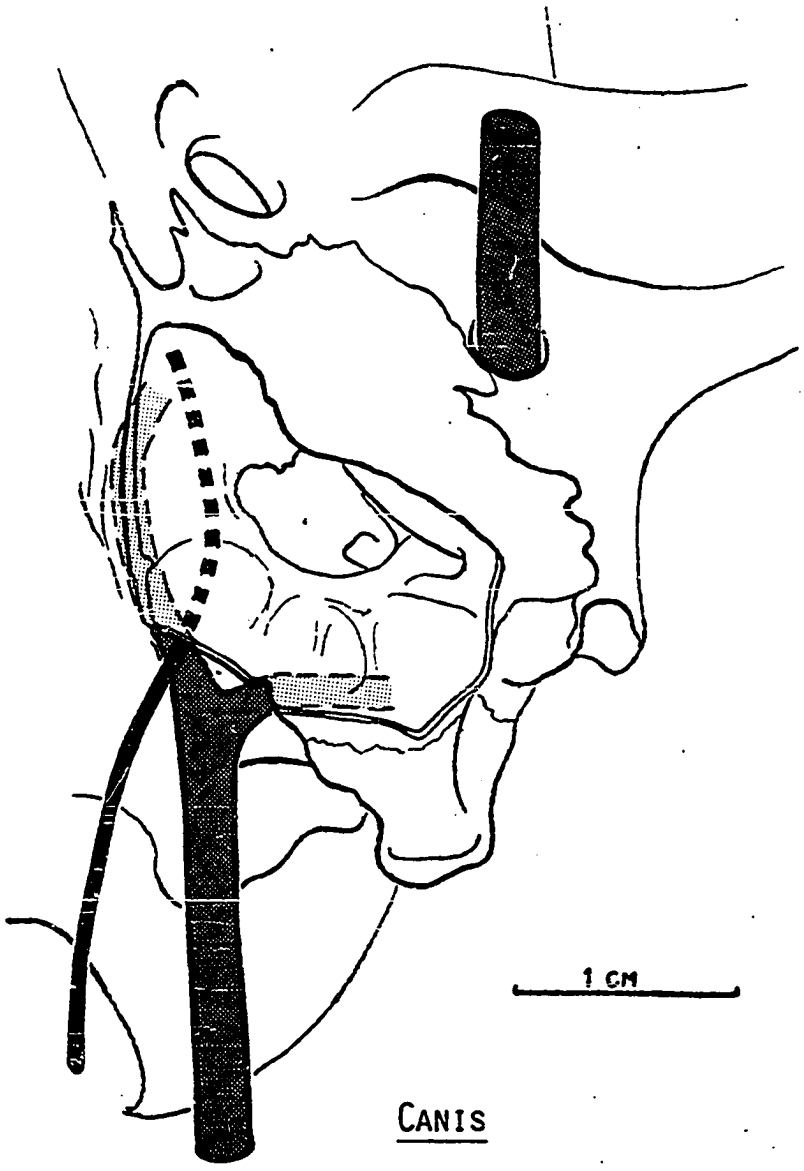
Figure 54: Three auditory regions, illustrating the relative horizontal positions of the carotid artery and the inferior petrosal sinus. In each case the internal carotid artery is black, solid extracranially and dashed intracranially. The veins are shaded, darker extracranially. The lateral fork of the 'Y' is the sigmoid sinus, and the medial, the inferior petrosal sinus. A) Pseudaelurus is reconstructed as a typical medium- to large-sized felid. B) Canis latrans exemplifies the canid, and even general caniform, condition. C) Dinictis is reconstructed here on the interpretation of the posterior foramen in the bulla being for an internal carotid artery rather than for a stapedial artery. Note that under my interpretation, the position of the inferior petrosal sinus is the same in all three.

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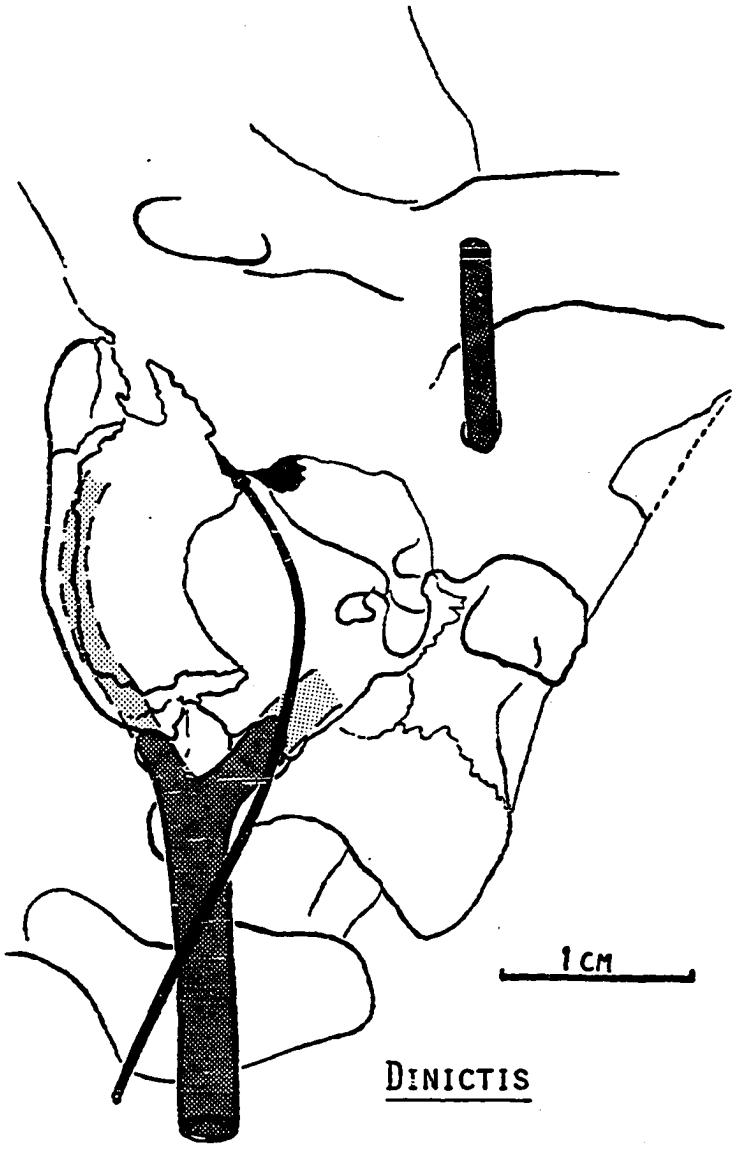
PSEUDAELURUS

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CANIS

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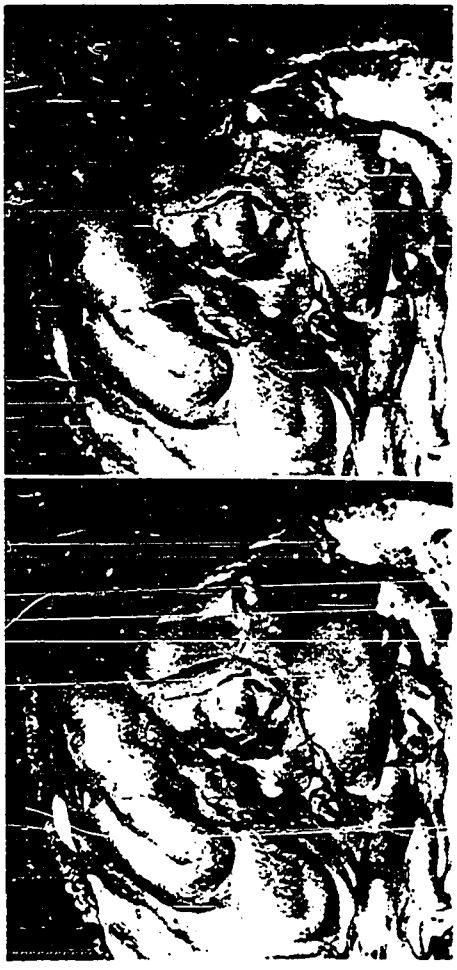


DINICTIS

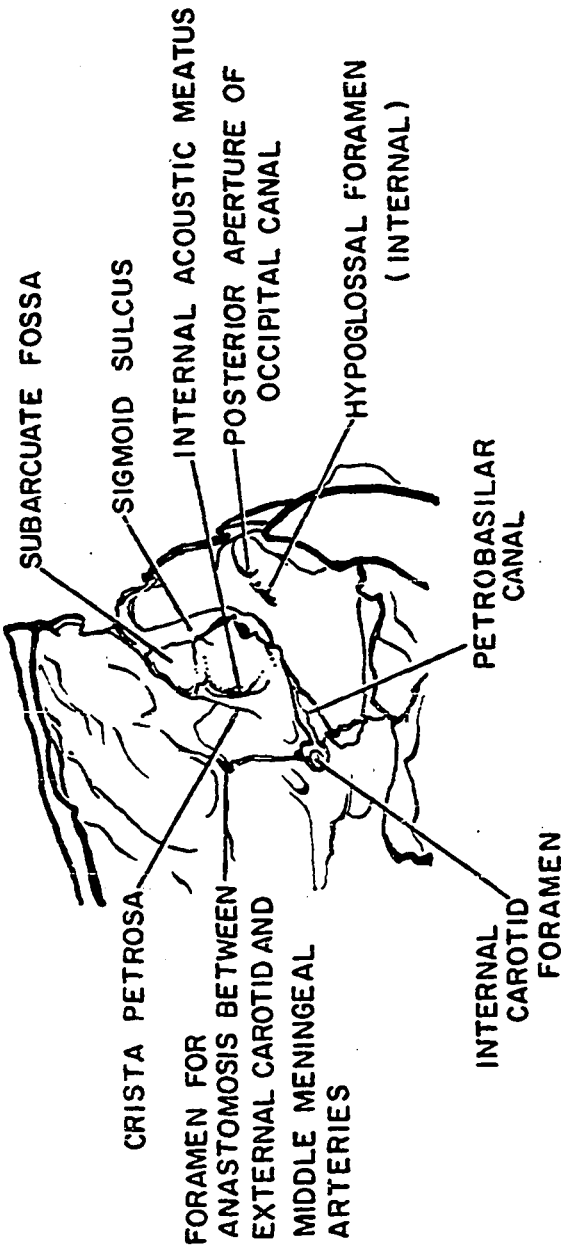
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Figure 55: Stereo pair showing the intracranial aspect of the right otic region of Taxidea americana, AMDM 15580, medial and slightly anterior view.

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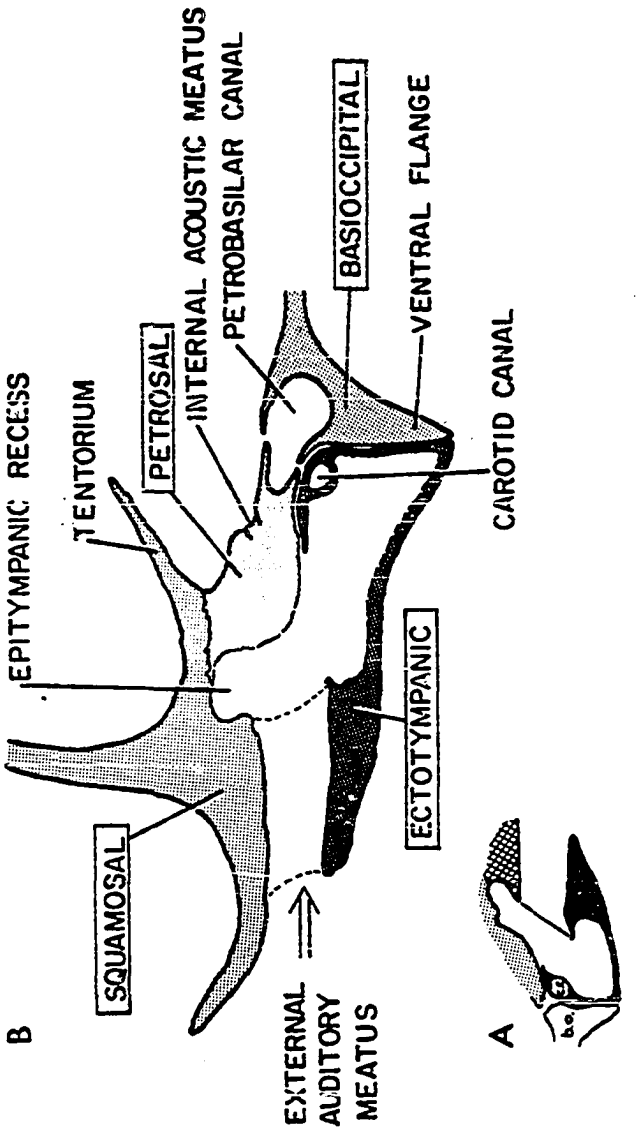
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Figure 56: Comparison of A) Van Kampen's (1905) cross section of Ursus with B) a diagram of the structure of the basioccipital and petrosal seen in Ursus americanus AMNH CA 35005.

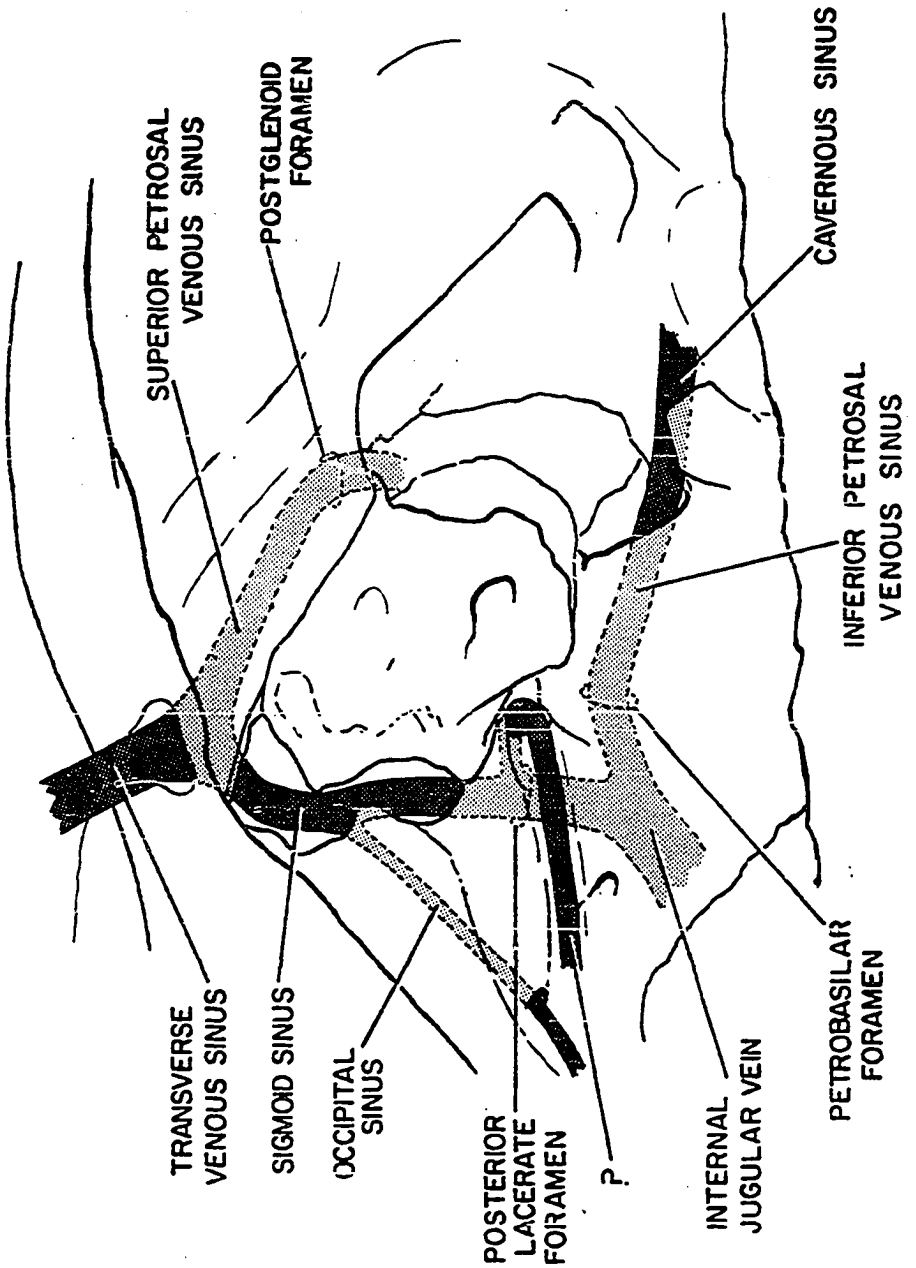
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Figure 57: A reconstruction of the veins on theintracranial side of the auditcry region in *Hoplophoneus* sp.

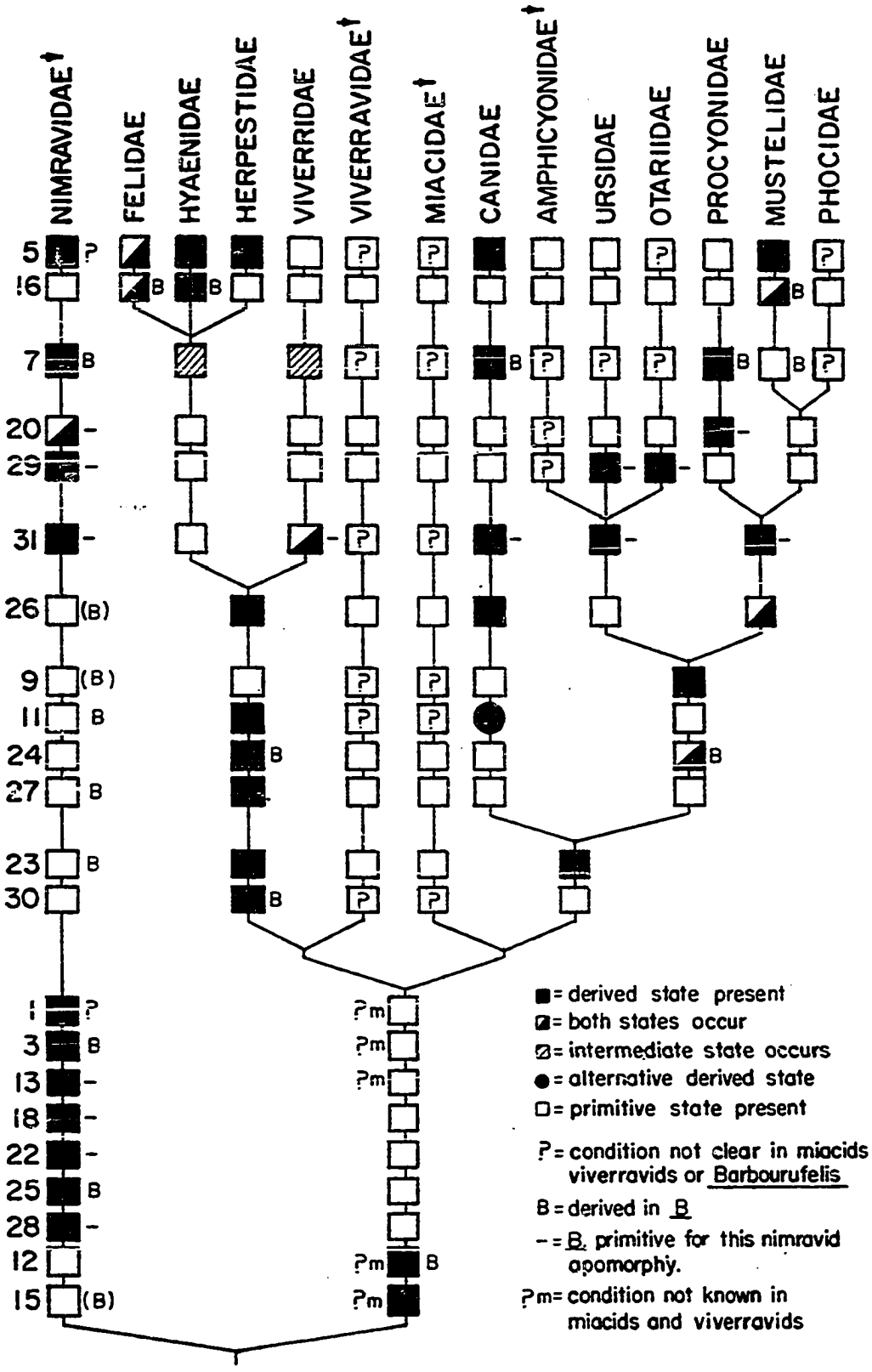
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Figure 58: The phylogeny of the Carnivora presented in Figure 7 with the distributions shown for those characters that my analysis concluded were informative; the Nimravidae are placed on this phylogeny to minimize the number of convergences or reversals necessary to explain their morphology (exclusive of Barbourofelis). The condition of these features in Barbourofelis is summarized as a function of the derived state for each feature: "B" next to a derived state, whether it occurs in Nimravidae or not, indicates that Barbourofelis also displays that derived condition. A "-" next to a derived condition signifies that Barbourofelis lacks a derived state found in the other nimravids and sometimes other carnivorans. Finally, a "(B)" flags those characters whose condition in nimravids and also Barbourofelis is primitive relative to that in some other taxon or taxa within the Carnivora, and therefore do not provide evidence for any specific relationship between Barbourofelis and anything else within the order.

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